

**Population dynamics and viability of the federally listed population of Steller's Eiders**

by

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## Abstract

For many species, uncertainty may intervene in accurately estimating population size, trend, and demographic parameters. Bayesian state-space models provide a convenient framework to account for multiple sources of uncertainty while remaining flexible to model structure and available data. We explored the efficacy this approach with Sequential Importance Sampling/Resampling for estimation of population size and demographic parameters. We then applied these methods to analyze multiple models of population process for Alaskan breeding Steller's eiders. Results strongly support that the Alaskan breeding population experiences population level non-breeding, and is open to exchange with the Russian-Pacific breeding population. Using this model of population process, we sought to assess viability of the Alaskan breeding population of Steller's eiders. Due to immigration, the Alaskan breeding population is under no risk of permanent extinction. However, it is likely that this population will continue to be present in low and highly variable numbers on the breeding grounds in Alaska.

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## **Chapter 1:**

### **Effects of model complexity and priors on estimation using Sequential Importance**

#### **Sampling/Resampling for species conservation**

##### **Abstract**

We examined the effects of complexity and priors on the accuracy of models used to estimate ecological and observational processes, and to make predictions regarding population size and structure. State-space models are useful for estimating complex, unobservable population processes and making predictions about future populations based on limited data. To better understand the utility of state space models in evaluating population dynamics, we used them in a Bayesian framework and compared the accuracy of models with differing complexity, with and without informative priors using sequential importance sampling/resampling (SISR). Count data were simulated for 25 years using known parameters and observation process for each model. We used kernel smoothing to reduce the effect of particle depletion, which is common when estimating both states and parameters with SISR. Models using informative priors estimated parameter values and population size with greater accuracy than their non-informative counterparts. While the estimates of population size and trend did not suffer greatly in models using non-informative priors, the algorithm was unable to accurately estimate demographic parameters. This model framework provides reasonable estimates of population size when little to no information is available; however, when information on some vital rates is available, SISR can be used to obtain more precise estimates of population size and process. Incorporating model complexity such as that required by structured populations with stage-specific vital rates



affects precision and accuracy when estimating latent population variables and predicting population dynamics. These results are important to consider when designing monitoring programs and conservation efforts requiring management of specific population segments.

## **Introduction**

Scientists and managers are frequently tasked with making management decisions for wildlife and fisheries populations using very little data to estimate population state and underlying demographic processes. To properly address conservation, managers often need a comprehensive understanding of the full state space, including; population structure, abundance, trend, and vital rates. For many species, uncertainty may intervene in accurately modelling state variables and these population processes. Models typically account for environmental and ecological uncertainty, also known as process uncertainty; however, this is rarely an adequate representation of the data, which are shaped by an observation process. Failing to adequately account for observation process, or measurement uncertainty, can lead to making poor management and policy decisions and may have profound impacts on the species of concern (Williams et al. 2002).

Typically, researchers and managers are only able to collect count data and some vital rate information on animal populations due to monitoring costs or difficulty in detecting species. This makes fitting models of population dynamics to the available counts challenging due to imperfect detection and process uncertainty (Hostetler and Chandler 2015, King et al. 2010). State-space models (SSM) provide a framework that can account for multiple sources of uncertainty while remaining flexible to model structure and available data. Thus, they can account for uncertainty through the state process model and observation process model which

link a time series of counts to the processes that affect population state. The state-space model framework is particularly advantageous because biologically plausible population processes and structure can be incorporated and key biological parameters can be estimated as latent variables, while explicitly acknowledging uncertainty in population and detection processes (Buckland et al. 2004, Thomas et al. 2005).

State-space models have been used to estimate biomass and make stock assessments of fish (Meyer and Millar 1999, Millar and Meyer 2000, Newman 1998), to estimate juvenile out-migration of salmon (Newman and Lindley 2006), to estimate demographic parameters and population size of birds and large mammals (Besbeas et al. 2002, Thomas et al. 2005, Trenkel et al. 2000), to estimate spatial and temporal variance in abundance of birds (Hostetler and Chandler 2015), and to estimate seasonal fluctuations of abundance and density dependent feedbacks of small mammals (Wang and Getz 2007). Central to each of these analyses is the availability of count data and little knowledge of demographic parameters and population size. Deducing information about demographic and observation processes without empirical data is notably beneficial considering the costs typically associated with collecting data on biological process and the time constraints managers' face when making decisions. Although the flexibility of state-space models is invaluable to researchers and managers attempting to better understand demographic processes and estimate the current and future states of the population in question, the effect of incorporating a high degree of complexity on the accuracy of estimates of the underlying process is unclear. The examples above used relatively complex state and observation process models, however, none of them explicitly address the effects of that level of complexity.

Conventional state-space models make assumptions of normality for the state process, and linear relationships between observations and the process model (Brooks et al. 2004,

Newman et al. 2006). Although computationally simpler, these assumptions are often not realistic representations of stochastic population dynamics (Brooks et al. 2004, Hostetler and Chandler 2015, Newman et al. 2006). Sequential Monte Carlo methods (or particle filtering), such as sequential importance sampling/resampling (SISR) have made non-linear population dynamics modelling more feasible (Doucet et al. 2001, Liu and Chen 1998, Liu and West 2001, Newman et al. 2006). SISR is the process of positing the uncertainty in population state, and the parameters influencing demographic and observation processes, then filtering them based on their likelihood given count data in a sequential process. Recent applications of SISR methods in animal population modelling include models for red deer (*Cervus elaphus*) (Trenkel et al. 2000), grey seals (*Halichoerus grypus*) (Thomas et al. 2005), and chinook salmon (*Oncorhynchus tshawytscha*) (Newman and Lindley 2006, Newman et al. 2006). SISR is feasible with both known and latent variables, making it particularly useful when little is known about population process (Buckland et al. 2004).

To better understand the utility of SSM's, we used them in a Bayesian framework and assessed the SISR algorithm's ability to estimate both population size and demographic parameters in models of differing complexity using informative and non-informative priors. Using simple models that only include the observable portion of the population ensures that all parameters are not conflated and therefore identifiable and estimable. While simple models may be useful to answer some questions regarding population dynamics, they may fail to accurately describe the underlying population processes or structure. Incorporating additional complexity in a model may increase understanding of population ecology and may be critical in addressing conservation objectives that focus on a particular population segment or demographic process, but additional complexity may lead to a higher degree of parameter conflation. Incorporating

appropriate, informative priors and constraints on parameters may reduce parameter conflation, improve accuracy and precision of posterior estimates, and allow for more complex process models when they are needed (Bailey et al. 2010, Morris et al. 2015). Model complexity is of particular interest due to common issues associated with partial observability in most population surveys. Segments of a population may be unobservable due to a large geographic range or life history strategies that preclude them from surveys (Bailey et al. 2010, King et al. 2010). The lack of information for these segments of the state space make it difficult to model the population process and can lead to parameter identifiability issues (King et al. 2010). We aimed to investigate the consequences of model complexity and the use of priors on obtaining accurate and useful information for modelling populations for conservation.

## **Methods**

### *State-Space Models*

The state process model describes the true, but unknown state of a population through a time series, and the observation process links the time-series abundance monitoring data to the state process. The state process is an unobservable vector, in this case representing the abundances of each population segment and is denoted as  $\mathbf{n}_{it}$ ,  $t = 0, 1, \dots, T$ ,  $i = 1, 2, \dots, I$ , where  $t$  is time and  $i$  represents the segment of the population. The state process is composed of stochastic sub processes that make up the population model and is first-order Markov; that is, the distribution of  $\mathbf{n}_{it}$  is dependent only on  $\mathbf{n}_{it-1}$  and the model parameters. Population models can be composed of any number of sub processes that advance  $\mathbf{n}_{it-1}$  to  $\mathbf{n}_{it}$ . The observation process, denoted as  $\mathbf{y}_{it}$ , where  $t = 0, 1, \dots, T$ , and  $i = 1, 2, \dots, I$ , is an observable vector and is a function of the state process. The observation process may include survey data for each segment of the

population or only for a subset of the population and is typically stochastic but can also be deterministic. The complete state-space model can be defined as three probability distribution functions (pdfs):

Initial state pdf:  $g_0(n_{i0}|\theta)$

State process pdf:  $g_{it}(n_{it}|n_{i0:t-1}, \theta)$

Observation process pdf:  $f_{it}(y_{it}|n_{it}, \theta)$

where  $t = 1, 2, \dots, T$ ,  $i = 1, 2, \dots, I$ , and  $\theta$  is a vector of model parameters. Using this information, we can make inferences about both  $n_{it}$  and  $\theta$ , conditional on the observed data in a Bayesian framework. Therefore, we also identify a prior distribution on  $\theta$ :

Prior pdf ( $\theta$ ):  $g_0(\theta)$ .

### *Population Dynamics Models*

We chose to work with three models of differing complexity to determine how these methods worked at increasing levels of model structure. Model formulation is directly linked to the purpose of the modelling effort, or questions asked about the population. As models become more complex, they may provide more insight than a simpler model. Therefore, we chose to investigate models with differing complexity in order to explore the utility of these methods in providing accurate information given what data is available. The first state process model was a simple birth and death model:

$$n_{t+1} = (n_t * S_t) + (n_t * S_t * f_t)$$

where  $S$  is survival and  $f$  is fertility. The observation process for model 1 is

$$y_t = n_t * p$$

where  $y_t$  is the observed count and  $p$  is detection probability. We assume detection ( $p$ ) is known with some error

$$p \sim \text{beta}(\alpha, \beta)$$

with shape parameters  $\alpha = 279.7$ , and  $\beta = 652.6$ , which gives us a distribution with  $\mu = 0.30$ , and  $\sigma = 0.015$ .

The second state process model is a two-sex, two-stage structured matrix model:

$$\begin{bmatrix} n_{jf} \\ n_{af} \\ n_{jm} \\ n_{am} \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & f_f & 0 & 0 \\ S_{jf} & S_{af} & 0 & 0 \\ 0 & f_m & 0 & 0 \\ 0 & 0 & S_{jm} & S_{am} \end{bmatrix} \begin{bmatrix} n_{jf} \\ n_{af} \\ n_{jm} \\ n_{am} \end{bmatrix}_t$$

where  $S$  is the survival rate of juveniles ( $j$ ) and adults ( $a$ ) of females ( $f$ ) and males ( $m$ ), and  $f$  is fertility for females ( $f$ ) and males ( $m$ ) with each parameter allowed to vary independently. The observation process for model 2 is

$$\begin{bmatrix} y_{jf} \\ y_{af} \\ y_{jm} \\ y_{am} \end{bmatrix}_t = \begin{bmatrix} n_{jf} \\ n_{af} \\ n_{jm} \\ n_{am} \end{bmatrix}_t * [p_{jf} \quad p_{af} \quad p_{jm} \quad p_{am}]$$

where the probability of detecting juveniles is  $p_{jf,jm} = 0$  and therefore  $y_{jf,jm} = 0$ . Probability of detecting adults is

$$p_{af,am} \sim \text{beta}(\alpha, \beta).$$

Again, we assume detection ( $p$ ) is known with the same shape parameters and thus the same mean and standard deviation as used in model 1.

The third model was constructed using the same framework as model 2, with added parameter constraints to reduce conflation. In this model we assumed adult female survival is a proportion of adult male survival, due to decreased survival in reproductively active females (Table 1). For many species, it is typical for breeding females to have lower survival than males

due to the physiological cost and increased predation risk associated with reproduction (Erikstad et al. 1998, Ghalambor and Martin 2001, Stearns 1976, Williams 1966). Juvenile survival was set to be proportional to adult female survival, because young animals tend to have decreased survival rates due to inexperience (Table 1). Juvenile survival and fertility were not allowed to vary independently, and were set equal between the sexes (Table 1). The parameter values are indicated by priors that are assumed to be a known proportion of the observable segments of the population, therefore reducing parameter redundancy in the model (Bailey et al. 2010, King et al. 2010). The observation process for model 3 is identical to the observation process for model 2.

Count data were simulated as annual abundance surveys over 25 years for each model. Observations were simulated using an initial population size with  $\mu = 1000$  and  $\sigma = 80$ , known parameter values, or “truth” (Table 1), and a deterministic observation process where  $p = 0.3$  for the observable segment(s) of the population. The values denoted as “truth” would be compared against the posterior mean estimates to determine the accuracy and precision with which the demographic parameters were estimated using SISR. Each model was run using both informative and non-informative priors to determine the effect of prior information on the posterior estimates (Figure 1, Table 1). Non-informative priors were beta distributed with shape parameters  $\alpha = 1, \beta = 1$  as a uniform flat distribution across the parameter space. This type of prior is used when there is no information on the vital rate and allows for any value between the minimum and maximum to be chosen. In this modelling effort, we chose to formulate models and priors based on the assumption that the model species is characteristic of a K-selected species, with high survival and low fertility. Informative prior distributions were chosen to be reflective of a great deal of uncertainty in the parameter values, while still being representative of the general life history of the species (Figure 1). Posterior estimates from each model run with

non-informative and informative priors were compared to the “true” values that were used to simulate the data in order to identify the circumstances under which these methods provided the most accurate and precise results.

### *Sequential Importance Sampling/Resampling with Kernel Smoothing*

Sequential Monte Carlo methods such as sequential importance sampling are used to solve Bayesian filtering problems when models and observations are non-linear and non-Gaussian (Doucet et al. 2001, Liu and Chen 1998). The objective of this method is to estimate the posterior distribution of population size and demographic parameters conditional on the observation. Direct sampling of the posterior or target pdf  $p(x)$  is typically not feasible, and therefore sequential importance sampling is used to generate samples from a trial pdf  $q(x)$  that is possible to sample (Doucet et al. 2001). For simplicity and ease of calculation, we chose to set the trial pdf  $q(x)$  equal to the state pdf  $g_t(n_t|n_{0:t-1}, \theta)$ . The evolution of the state pdf through time  $t$  is based on the processes defined in the population process model, defined in Section 2.2.

To initialize the sequential importance sampling/resampling algorithm, we generated  $J$  sets of  $n_0$  and the parameters  $\theta$ , or “particles”, from the initial state distribution  $g_0(n_0|\theta)$ , and joint prior distribution on the parameters,  $g_0(\theta)$  and set  $t = 1$ . In our models, we chose  $J = 100,000$  particles, where  $j = 1, \dots, J$ , and used an algorithm based on the steps described below.

*Step 1.* Generate a sample of size  $N$  particles from the trial pdf,  $q(n_t)$  which we set equal to the state pdf  $g_t(n_t|n_{0:t-1}, \theta)$ .

*Step 2.* Calculate weights ( $w_t^j$ ) for each particle. Because we set the trial pdf,  $q(n_t)$ , equal to the state pdf,  $g_t(n_t|n_{0:t-1}, \theta)$ , the weights are proportional to the observation pdf,  $f_t(y_t|n_t, \theta)$ .



Therefore, the resampling selects the best fit sets of values, or particles, according to the observed data:

$$w_t^j \propto \frac{f_t(y_t | n_t^j, \theta^j) * g_t(n_t^j | n_{0:t-1}^j, \theta^j)}{q(n_t^j)}$$

*Step 3.* Resample the particles with replacement, according to the calculated weights,  $w_t^j$ .

*Step 4.* For each particle, kernel smooth the parameter distributions  $\theta^j$  using combinations of the original values and simulated values from a multivariate normal distribution (West 1993a,b; see explanation below).

*Step 5.* For each particle,  $n_t$  is redefined as the weighted resampled states (from step 3) and the parameters  $\theta^j$  are redefined as the resampled and smoothed parameter estimates (from steps 3 and 4).

*Step 6.* The algorithm uses these resampled and smoothed values at the next time step and continues updating sequentially following Steps 2-6, using a first-order Markov process through the last time step of available observation data.

Due to the weighted resampling that occurs in Step 2, SISR can suffer from a phenomenon known as particle depletion which can lead to biased posterior estimates (Liu and West 2001). Therefore, the number of particles chosen to initialize the algorithm must be very large because the number of unique particles is successively reduced at each time step during the resampling process (Newman et al. 2006). If there are very few particles left at any time step, their distribution becomes heavily skewed. Only a few particles will have a measurable importance weight and the resulting distribution will fail to accurately represent the posterior distribution (Liu and West 2001). The first technique to mitigate the issue of particle depletion is to include bootstrap resampling (Gordon et al. 1993). In our model this takes place directly after

the particles are assigned weights. The purpose of this step is to remove particles with infinitesimal weight, and to replicate the particles that have high importance weights (Gordon et al. 1993). An additional technique that deals with particle depletion is kernel smoothing of the parameter distributions. Kernel smoothing introduces new parameter values near to those that remain after bootstrapping. This particular method developed by West (1993a,b) smooths the parameter distributions using a multivariate normal distribution ( $N$ )

$$p(\theta|D_t) \approx \sum_{j=1}^J w_t^{(j)} N(\theta|m_t^{(j)}, h^2 V_t)$$

where at time  $t$ , we have current posterior parameter samples  $\theta_t^{(j)}$  and weights  $w_t^{(j)}, j = 1, \dots, J$ , which provide a discrete Monte Carlo approximation to the posterior distribution  $p(\theta|D_t)$  (Liu and West 2001). The Monte Carlo posterior mean  $m_t$  and variance matrix  $V_t$  of  $p(\theta|D_t)$  are calculated from the Monte Carlo sample  $\theta_t^{(j)}$  with weights  $w_t^{(j)}$  (Liu and West 2001). Kernel scaling uses  $V_t$ , the Monte Carlo posterior variance and scales according to  $h$ , the smoothing parameter (Liu and West 2001). The value of  $h$  can be between 0 and 1, when  $h = 1$  there is no smoothing, and when  $h = 0$  there is maximum smoothing. We chose  $h = 0.9$  as the smoothing parameter, similar to Newman et al. (2006). To correct for over dispersion, West (1993a,b) introduced shrinkage of the kernel locations

$$m_t^{(j)} = a\theta_t^{(j)} + (1 - a)\bar{\theta}_t$$

where  $a = \sqrt{1 - h^2}$ . The resulting normal mixture retains the mean  $\bar{\theta}_t$  and the variance  $V_t$  is corrected for over dispersion (Liu and West 2001). Kernel smoothing replaces the duplicated values that remain after resampling with slightly perturbed and typically unique values, increasing the number of particles available at the next time step. The model parameters were mapped to the real number line for multivariate normal kernel smoothing, and then back-

transformed after smoothing. This transformation constrained the parameter space for survival to values between 0 and 1, however, with the additional perturbation the parameter space for fertility was allowed to be between 0 and 3, which is slightly larger than the prior (Tables 1,2). Additional information on kernel smoothing and other particle filter improvements can be found in Doucet et al. (2001). Each model was coded using MATLAB version 8.4.0.15 (The Mathworks, Inc., Natick, Massachusetts, United States). The use of trade names or products does not constitute endorsement by the U.S. Government.

## **Results**

The posterior distributions of population size included truth and the simulated population state, within the 95% credible intervals, regardless of model complexity or prior type (Figure 2). Prior information on parameters had little effect on the estimation of population size in any model, the only notable effect being wider credible intervals around the estimates from simulations with non-informative priors (Figure 2). The fit of population size to each model estimates appear to be acceptable, with two exceptions. Over the time series, the non-informative version of model 2 was unable to track closely with the true population trend. It consistently overestimated abundance and accuracy did not increase over time (Figure 2). In addition, population size was estimated with large credible intervals, which did not contract over time, as they did in the other models. It is clear that the algorithm applied relatively high weights to sets of parameter values that were implausible and was unable to estimate population size accurately. The estimates from the non-informative version of model 3 were initially far from truth, but the algorithm was able to learn and became more accurate. At each time step the estimates of population size became nearer to truth and credible intervals shrunk as a result. This

demonstrates that the algorithm was able to overcome the lack of information regarding parameter values, but required several time steps to learn the correct values.

Model 1 provided accurate results using both informative and non-informative priors, likely because there were only two parameters to estimate and there were no unobservable states in the population. Model 2 accurately estimated parameter values with informative priors, however using non-informative priors led the model to overestimate fertility and adult survival, and underestimate juvenile survival (Table 2). The state process of model 2 included multiple latent variables that were conflated. When appropriate prior information was included, the posterior estimates of parameters and population size provided accurate estimates of the population process. However, lack of prior information and data for multiple parameters caused the algorithm to over-estimate the likelihood of unrealistic combinations of parameters, leading to inaccurate posterior estimates of both parameters and population size. When using a more complex model, similar to model 2, it is necessary to incorporate appropriate prior information, data on each segment of the population, or both. The additional constraints on the parameters in model 3 resulted in accurate posterior estimates from both the informative and non-informative versions of the models (Table 2). Posterior estimates for each model using non-informative priors resulted in estimates with greater uncertainty than their better-informed counterparts. The lack of information allows the algorithm to heavily weight any combination of parameters that could reasonably lead to the observation; however, with no constraints on the parameters the model over-estimated the likelihoods of combinations of parameter values that were far from accurate. The inaccuracy of the results is most noticeable in the posterior estimates of juvenile survival and fertility.

## Discussion

While both Sequential Monte Carlo and Markov chain Monte Carlo (MCMC) are proven methods available for fitting Bayesian SSM, we chose SISR with kernel smoothing due to its ease of implementation (Godsill et al. 2004, Newman et al. 2006, Newman et al. 2009). We agree with others who found that these methods are suitable for fitting time series abundance data, filtering non-linear models, and non-Gaussian error structures (Trenkel et al. 2000, Newman and Lindley 2006, Newman et al. 2006).

The performance of each model was assessed by the accuracy and precision with which the population size and parameters were estimated. Models with informative priors consistently estimated posterior parameters values with greater accuracy and precision than their non-informative counterparts. Population size and trend were accurately estimated in every model except the non-informative prior version of model 2 (Figure 2). Because the parameters in model 2 were allowed to vary independently and these parameters are inherently conflated, the abundance and parameter estimates were inaccurate. By comparison, using informative priors for model 2 or constraining the parameters as in model 3, results in accurate estimates of parameters and abundance. Thus, we suggest for populations with complex structure, researchers attempt to identify appropriate priors and covariance for these parameters.

The parameters we used to simulate truth were chosen to emulate a relatively long-lived animal with low fertility and delayed maturation. For example, lesser snow goose populations have been modelled using annual survival rates of 0.80 and fertilities greater than 0.68 (Cooch et al. 2001). We chose priors to reflect biologically plausible values and relatively great uncertainty. It is conceivable that an analyst would choose informed priors similar to the ones we used (Table 1) based on published literature and knowledge of the life history strategies of a

species. These were not particularly strong priors (Figure 1) and essentially worked to steer the algorithm away from over-weighting parameter combinations that would not be plausible given the life history of the species. The models run with non-informative priors resulted in posterior parameter estimates that were not realistic for this population, but still estimated population size relatively well (Table 2, Figure 2). The issues with using non-informative priors are specifically apparent in models 2 and 3, which had unobservable segments of the population. In these models the algorithm has no prior information or observation data for the juvenile segments of the population. This allows the algorithm to apply a large weight to any possible combination of values resulting in a likely estimate of the observation and results in inaccurate posteriors for the vital rates (Table 2). The only case in which non-informative priors resulted in biologically reasonable parameter estimates was in model 1 (Table 2). This is most likely because the entire population was considered observable, rather than just a few segments. Therefore, the observed data used in the updating algorithm was the entire state space, which is not the case in the more complex models.

Parameters associated with population segments that were not observable had posterior estimates that were much more variable in all of the models suggesting a strong link between the ability to accurately estimate parameter values and the observation process. While these results are not particularly surprising, they do have serious implications for management and conservation. It is common to have unobservable segments of a population, due to large geographic extents, life history strategies, or species behavior. For example, many animal surveys are conducted on breeding grounds where juvenile animals are infrequently encountered (e.g. Waterfowl Breeding Population Surveys; Bowman et al. 2015). When there is a complete

lack of observations and information on vital rates for those population segments, SISR methods may be unable to provide sufficient data to inform management.

## **Conclusion**

SISR can be used to accurately estimate both population size and demographic parameters in models of differing complexity, given certain constraints on parameters, prior information on vital rates, and/or observation data on important life stages. The accuracy and precision of the algorithm is a function of the prior information provided for the parameters and the observability of the population segment associated with the parameters. These results suggest model complexity should be considered in terms of what objectives need to be met. For instance, models 1 and 3 were able to accurately estimate population size and trend using both informative and non-informative priors (Figure 2). However, each of the models estimated posterior parameter values with more precision and accuracy when initialized with informative priors versus non-informative priors (Table 2). If the only objective is to monitor population size and/or trend, then simple models using non-informative priors may provide sufficient insight. However, if the objectives include understanding population processes and demographic parameters, then more complex models and informative priors should be used.

While our models generally characterize a relatively long lived species, with high survival, low fertility, and a closed population, similar methods have been used to model open and closed populations of small mammals (Wang and Getz 2007), large mammals (Thomas et al. 2005, Trenkel et al. 2000), fish (Newman and Lindley 2006, Newman et al. 2006), and birds (Besbeas et al. 2002, Hostetler and Chandler 2015). The methods outlined here can be applied to open populations and species with different life history strategies by formulating appropriate

population process models. Some extensions may include a mixture of informative and non-informative priors, multiple surveys used for the observation process, hierarchical hyperparameters, and setting priors as a function of covariates (Brooks et al. 2004, Buckland et al. 2007, Hostetler and Chandler 2015, King et al. 2010, Newman and Lindley 2006, Newman et al. 2006, Thomas et al. 2005). However, models should be formulated depending on the objectives of the modelling effort and the information available on the population.

SISR can be a valuable tool for the effective management and conservation of animal populations; however, researchers and managers should be aware that when observations and vital rates are lacking for some segments of populations, estimates obtained using SISR may be inaccurate. This may be extremely important when conservation of those population segments is a critical objective. However, information can still be gleaned using simplistic models while simultaneously identifying areas in which to target monitoring efforts.

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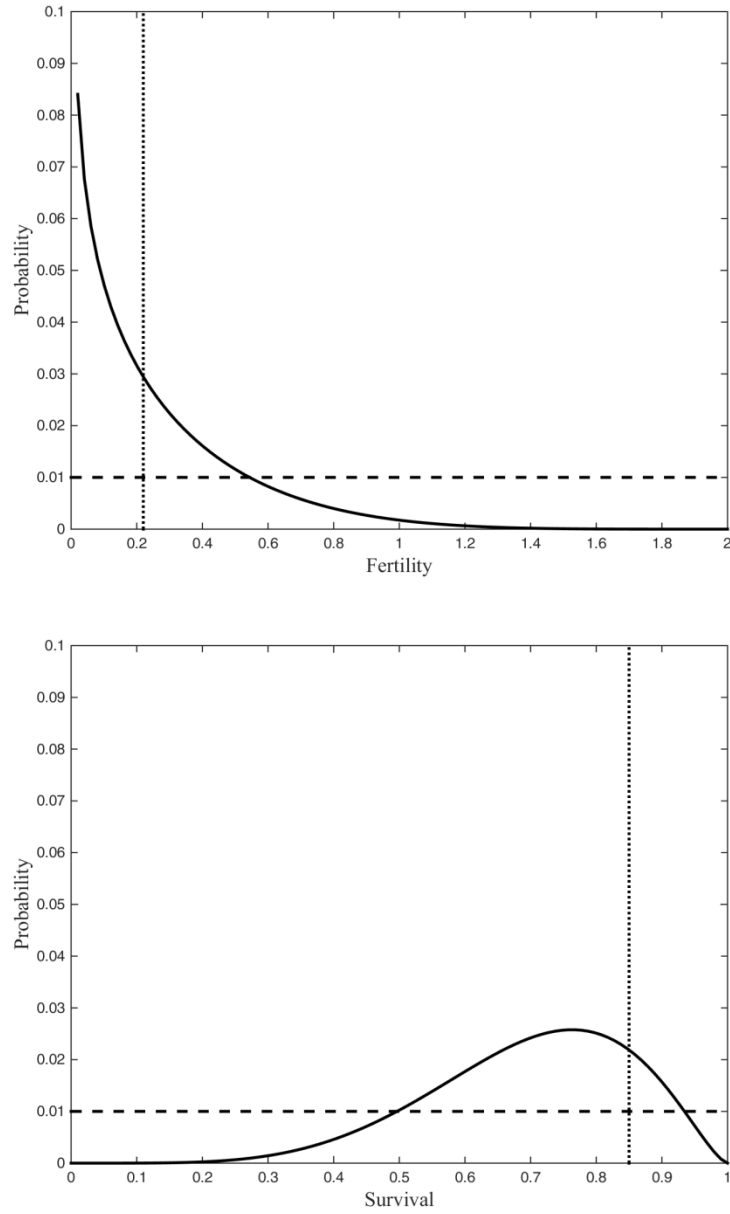
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## Tables and Figures

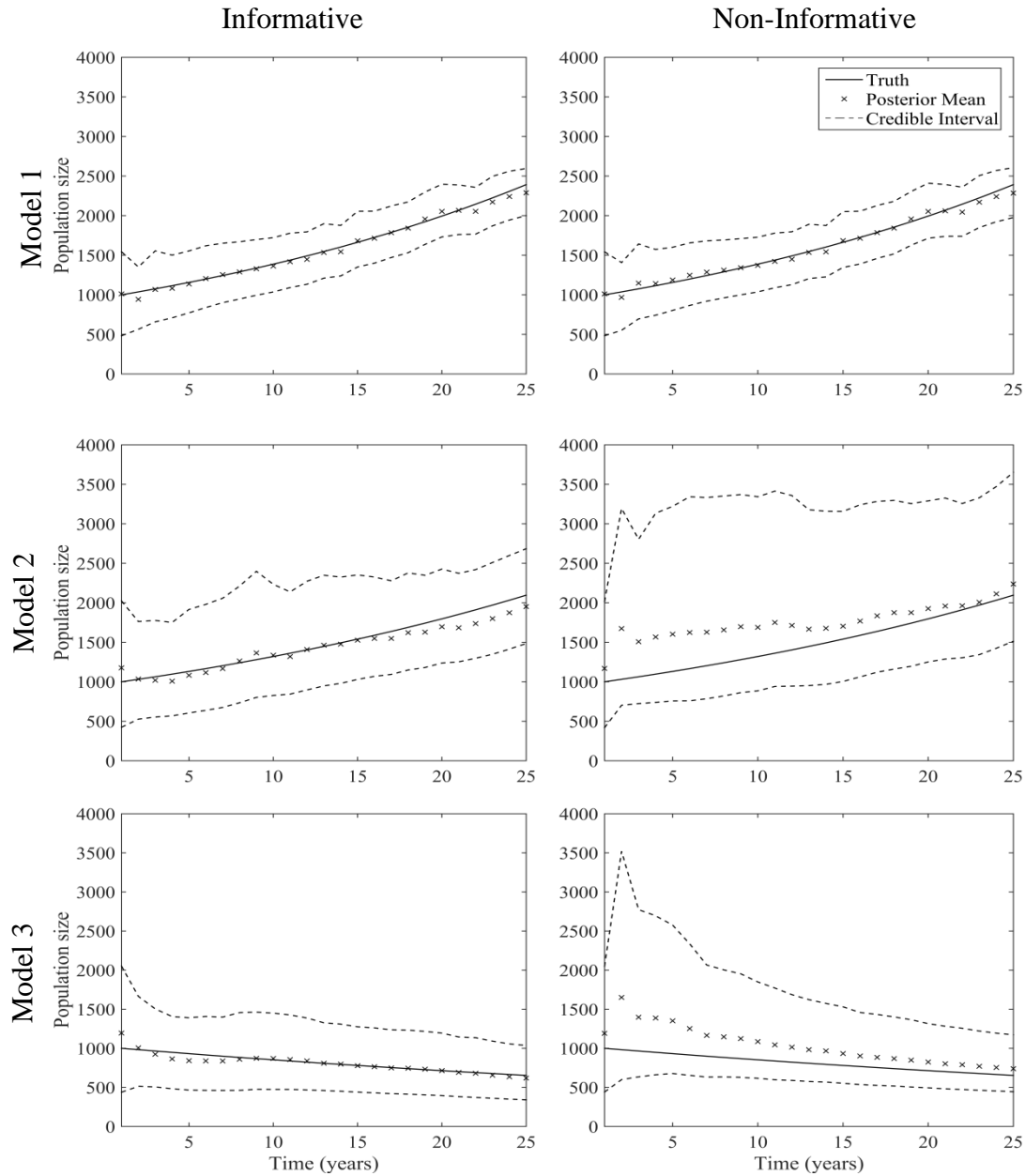
**Table 1.1.** Initial values used as parameters ( $\theta$ ) in population models and prior distributions. Truth was used to generate simulated observations for comparison to particles in the sequential importance sampling resampling algorithm, distributions can be seen in Figure 1.

$\theta$	Truth	Informative $\mu$	Informative $\sigma$	Informative $g_0(\theta)$	Non-Informative $g_0(\theta)$
<b>Model 1</b>					
$S$	0.85	0.70	0.25	<i>beta</i> (1.652, 0.708)	<i>beta</i> (1, 1)
$f$	0.22	0.25	0.25	<i>beta</i> (0.5, 1.5)	<i>beta</i> (1, 1)
<b>Model 2</b>					
$S_{jf}$	0.85	0.70	0.25	<i>beta</i> (1.652, 0.708)	<i>beta</i> (1, 1)
$S_{af}$	0.85	0.70	0.25	<i>beta</i> (1.652, 0.708)	<i>beta</i> (1, 1)
$S_{jm}$	0.85	0.70	0.25	<i>beta</i> (1.652, 0.708)	<i>beta</i> (1, 1)
$S_{am}$	0.85	0.70	0.25	<i>beta</i> (1.652, 0.708)	<i>beta</i> (1, 1)
$f_f$	0.22	0.25	0.25	<i>beta</i> (0.5, 1.5)	<i>beta</i> (1, 1)
$f_m$	0.22	0.25	0.25	<i>beta</i> (0.5, 1.5)	<i>beta</i> (1, 1)
<b>Model 3</b>					
$S_{jf,jm}$	0.77	0.64	0.25	0.95* $S_{af}$	0.95* $S_{af}$
$S_{af}$	0.81	0.67	0.25	0.95* $S_{am}$	0.95* $S_{am}$
$S_{am}$	0.85	0.70	0.25	<i>beta</i> (1.652, 0.708)	<i>beta</i> (1, 1)
$f_{m,f}$	0.22	0.25	0.25	<i>beta</i> (0.5, 1.5)	<i>beta</i> (1, 1)

*Notes:*  $f$  indicates sex specific fertility;  $S$  indicates sex and stage specific survival. Fertility ( $f$ ) was modelled using a stretched beta, minimum value = 0, maximum value = 2.



**Figure 1.1.** Prior distributions and truth for survival and fertility rates. Truth and prior distribution shape parameters, mean, and standard deviations are located in Table 1. Truth is denoted as the vertical line, non-informative prior distributions are the dashed lines, and the informative priors are the solid lines.



**Figure 1.2.** Comparison of true population size simulated over 25 years, posterior mean population size, and 95% credible interval for each model and prior type. Posterior means and credible intervals are results from the sequential importance sampling resampling process.

**Table 1.2.** Posterior mean ( $\mu$ ), 95% credible interval (CI), and truth for each parameter ( $\theta$ ) across all models and prior types compared using sequential importance sampling resampling.

$\theta$	Truth	Informative $\mu$ (95% CI)	Non-Informative $\mu$ (95% CI)
<b>Model 1</b>			
$S$	0.85	<b>0.80</b> (0.57-0.96)	<b>0.73</b> (0.51-0.98)
$f$	0.22	<b>0.32</b> (0.05-0.81)	<b>0.46</b> (0.04-0.97)
<b>Model 2</b>			
$S_{jf}$	0.85	<b>0.69</b> (0.37-0.91)	<b>0.29</b> (0.02-0.89)
$S_{af}$	0.85	<b>0.87</b> (0.73-0.96)	<b>0.81</b> (0.41-0.97)
$S_{jm}$	0.85	<b>0.69</b> (0.36-0.92)	<b>0.28</b> (0.02-0.87)
$S_{am}$	0.85	<b>0.91</b> (0.82-0.97)	<b>0.96</b> (0.89-0.99)
$f_f$	0.22	<b>0.21</b> (0.01-0.87)	<b>0.74</b> (0.10-2.53)
$f_m$	0.22	<b>0.21</b> (0.01-0.87)	<b>0.74</b> (0.08-2.93)
<b>Model 3</b>			
$S_{jf,jm}$	0.77	<b>0.79</b> (0.69-0.87)	<b>0.62</b> (0.51-0.73)
$S_{af}$	0.81	<b>0.83</b> (0.74-0.91)	<b>0.66</b> (0.54-0.77)
$S_{am}$	0.85	<b>0.88</b> (0.78-0.95)	<b>0.82</b> (0.51-0.97)
$f_{f,m}$	0.22	<b>0.16</b> (0.01-0.68)	<b>0.49</b> (0.15-1.16)

*Note:*  $S$  indicates sex and stage specific survival,  $f$  indicates sex specific fertility.

## Chapter 2:

### **Evaluating models of population process in a threatened population of Steller's eiders: A retrospective approach**

#### **Abstract**

The Alaskan breeding population of Steller's eiders (*Polysticta stelleri*) was listed as threatened under the Endangered Species Act in 1997 in response to perceived declines in abundance and breeding and nesting range. Aerial surveys suggest the breeding population is small and breeds in highly variable numbers, with zero birds counted in 5 of the last 25 years. The primary objective of this research is to evaluate competing population process models of Alaskan-breeding Steller's eiders through comparison of model projections to aerial survey data. To evaluate model efficacy and estimate demographic parameters, we used a Bayesian state-space modelling framework and fit each model to counts from the annual aerial surveys using sequential importance sampling/resampling. The results strongly support that the Alaskan breeding population experiences population level non-breeding events, and is open to exchange with the larger Russian-Pacific breeding population. Current recovery criteria for the Alaskan breeding population rely heavily on the ability to estimate population viability. Our results provide an informative model of the population process that can be used to examine future population states and assess the population in terms of the current recovery and reclassification criteria.



## Introduction

Steller's eiders (*Polysticta stelleri*) are small sea ducks that inhabit the Arctic and subarctic regions in Russia and Alaska (Frederickson 2001, Pearce et al. 2005). The Alaskan breeding population was listed as threatened under the Endangered Species Act in 1997 in response to a perceived decline in abundance throughout their breeding and nesting range (Federal Register 1997). The recovery team identified a critical need to estimate and reduce the extinction risk of this breeding population (U.S. Fish and Wildlife Service 2002). Assessing extinction risk requires a comprehensive understanding of population dynamics and underlying population processes, as well as the associated uncertainty. Sufficient information on a threatened species is particularly difficult to obtain, specifically for Steller's eiders. The remote nature of their nesting, breeding, wintering, and molting sites makes this species especially difficult to observe (Frederickson 2001). The lack of observability makes it challenging to accurately estimate demographic processes or population size and trend. Furthermore, there is additional uncertainty regarding how the Alaskan breeding population relates to the larger global population of Steller's eiders. The interaction between the global population and the much smaller Alaskan breeding population may have serious implications for population viability.

There are three geographically distinct breeding populations of Steller's eiders; the Russian-Atlantic population, Russian-Pacific population, and the Alaskan population (U.S. Fish and Wildlife Service 2002, Pearce et al. 2005). The Russian-Atlantic population nests in northern Norway and in Russia west of the Taimyr Peninsula, and winters in the Barents and Baltic seas (Nygard et al. 1988, 1995, Pearce et al. 2005, Petersen et al. 2006). The largest population is the Russian-Pacific population, which nests in Siberia east of the Taimyr Peninsula (Pearce et al. 2005). The smallest of the three populations is the Alaskan breeding population, which may

contain fewer than 600 individuals (Stehn and Platte 2009). This small breeding population nests on the Arctic Coastal Plain (ACP) of Alaska, primarily near the town of Barrow. Both the Russian-Pacific and Alaskan breeding populations congregate on the same molting and wintering areas along the Alaskan Peninsula (Martin et al. 2015, U.S. Fish and Wildlife Service 2002). They exhibit high rates of fidelity to specific molting areas in Alaska and pair bonding occurs on the wintering grounds (Flint and Herzog 1999). There are alternative hypotheses regarding closure between the Russian-Pacific and Alaskan breeding populations. Movement between these two populations could have serious implications for assessing extinction risk and recovery (Martin et al. 2015.) Determining if the Alaskan breeding population is open or closed to movement is a critical component to better understand the processes that govern this population.

Planning for the conservation and recovery of an imperiled species requires an assessment of population status. Like many threatened or endangered species, the Alaskan breeding population of Steller's eiders is monitored annually. Road-based and transect surveys for breeding pairs are conducted near the town of Barrow, Alaska (Obritschkewitsch et al. 2001, Safine 2013, Stehn et al 2013). Additionally, aerial surveys have been flown annually since 1989 along the ACP (Obritschkewitsch et al. 2001, Safine 2013, Stehn et al. 2013). These surveys indicate that the Alaskan breeding population is present in low and highly variable numbers (Stehn et al. 2013). Based on 25 years of aerial survey data from the ACP, the number of birds counted ranged from zero (in 5 years) up to 635 (SE 405) birds (Stehn et al. 2013). These variable counts make it particularly difficult to characterize a reliable population trend and the risk of extinction. Typically, the results of these annual surveys can be used to develop models and estimate population viability, however, highly variable counts, zero count years, and the large amount of uncertainty surrounding these counts makes it particularly challenging to

quantify viability. Furthermore, there is additional uncertainty regarding of demographic rates. Survival rates have been estimated for this species using birds marked on the molting grounds (Flint et al. 2000(b), Frost et al. 2013, Reynolds 2007). These studies typically included a large portion of non-breeding birds, and birds from both the Russian-Pacific and Alaskan breeding populations. While these studies provide a foundation for understanding survival rates for this species, demographic rates of the Alaskan breeding population are likely to differ from the birds studied on the molting sites.

A central problem in conserving a threatened or endangered species is the difficulty in properly quantifying uncertainty. For Steller's eiders, uncertainty in population process hinders the ability to accurately assess the population's extinction risk, which, for the Alaskan breeding population, must be  $< 1\%$  over 100 years to meet one of the criteria for down-listing (U.S. Fish and Wildlife Service 2002). A principal objective outlined in the recovery of this population was to gain a more comprehensive understanding of the dynamics of Alaskan breeding population and use this information to estimate the past, current, and future breeding population status (USFWS 2002). We sought to develop and identify explicit models of population processes to evaluate the status of the Alaskan breeding population. We used Bayesian state-space models to formally account for the multiple sources of uncertainty associated with the observation process, parameters, and population closure. Bayesian state-space models provided a flexible framework to explicitly account for uncertainty, which is particularly important when modelling a threatened species (e.g., Buckland et al 2004, Buckland et al. 2007, Dunham and Grand 2015 *in review*, Newman and Lindley 2006, Newman et al. 2006, Newman et al. 2009, Thomas et al. 2005).

It is vital to adequately account for uncertainty when making management and policy decisions for species of conservation concern. State-space models provide a convenient framework to explicitly acknowledge uncertainty in population and observation processes while simultaneously modelling biologically plausible population processes and estimating key demographic parameters (Buckland et al. 2004, Dunham and Grand *in review*, Thomas et al. 2005). This approach allowed for the direct comparison of multiple models of population process and fit each model to the available observation data from the aerial surveys. The sequential nature of the aerial survey data provided a convenient opportunity to employ sequential Monte Carlo methods, and more particularly Sequential Importance Sampling with Resampling (SISR), to fit process models to observation data. This method was appropriate for analyzing sequential data, and provided posterior estimates of demographic rates and population state at each time step (Newman et al. 2009). Therefore, we were able to incorporate time-varying or hierarchical parameters and estimate posterior distributions for each parameter after each time step (Newman et al. 2009). This was particularly important for this modelling effort because it allowed us to account for movement between the Russian-Pacific and Alaskan breeding populations. Additionally, we directly compared the results from each process model, after each time step, to determine which model of population process best fit the observational data. This approach provided us with the opportunity to explicitly account for process uncertainty, observation uncertainty, and model uncertainty, while simultaneously providing estimates of demographic rates and identifying the most appropriate population process model.

We developed four competing models to reflect alternative hypotheses and uncertainty in the underlying population processes. Our primary objective was to evaluate support, based on count data, for competing models that represent hypotheses for the population dynamics of the

Alaskan breeding population of Steller's eiders. Additionally, because we used SISR, we also were able to estimate underlying demographic rates.

## **Methods**

### *Survey Methods*

Given the importance of the ACP for breeding waterfowl, the U.S. Fish and Wildlife Service Division of Migratory Bird Management conducted aerial surveys sampling roughly 60,000 km<sup>2</sup> in the ACP to monitor the distribution, abundance, and trend of bird species. The original ACP surveys were flown from 1986 – 2006, monitoring many avian species in the area. Following the listing of the spectacled eider (*Somateria fischeri*) in 1992, the North Slope Eider (NSE) survey was established and flown through 2006, monitoring primarily spectacled and Steller's eiders. In 2007, the ACP and NSE surveys were merged. Stehn et al. (2013) conducted analyses to combine the data sets from all surveys from 1986 to 2013 and determine population trends of the monitored species. The aerial survey data used in our research to evaluate population process models were taken from the combined survey results in Stehn et al. (2013). The data set used in our analysis of population process models used the number of indicated breeding Steller's eiders estimated each year from 1989 to 2013. Stehn et al. (2013) estimated the number of indicated breeding birds as

$$((2 * \text{number of single birds}) + (2 * \text{number of pairs})).$$

The number of single birds is doubled under the assumption that only pairs are present on the surveyed area. This number was corrected using an adjustment ratio according to timing of the survey, the percentage of the area sampled, and the stratum to account for the average relative difference between observed densities amongst the different survey types. This included differences in seasonal chronology, survey timing, weather conditions, movement of birds, and

observers (Stehn et al. 2013). The adjustment ratio converted aerial index densities observed on the ACP survey as if they had been observed on the NSE survey (Stehn et al. 2013). Therefore, the data set used in our analysis to evaluate models of population process correspond to the time while eiders are in breeding pairs, before the males depart, consequently corresponding to a pre-breeding census and is treated as such in our models and analysis. The adjustment ratios used to combine the results from the surveys are not indicative of detection probability, which was accounted for in our model below. Additional information on timing, stratification, sampling, and analysis of these surveys and the data collected is available in Stehn et al. (2013).

### *State-Space Model Formulation*

Bayesian state-space models (SSM) provide a flexible modeling framework to account for multiple sources of uncertainty (Brooks et al. 2004). State-space models account for uncertainty through a state process and observation process which link time series of counts to the underlying processes that affect the population state (Buckland et al. 2004, Newman 1998, Thomas et al. 2005). We used a SSM framework and developed four competing state process models to examine the possibilities of Steller’s eider population dynamics. The general Bayesian state-space modelling framework consists of four probability distribution functions (pdfs):

Initial state pdf:  $g_0(N_0|\theta)$

State process pdf:  $g_t(N_t|N_{0:t-1}, \theta)$

Observation process pdf:  $f_t(c_t|N_t, \theta)$

Prior pdf:  $g_0(\theta)$

where  $t = 1, 2, \dots, T$  and  $\theta$  is a vector of model parameters. Using this information, we can make inferences about both  $N_t$  and  $\theta$ , conditional on the observed data.

The full state process model was defined as:

$$\begin{bmatrix} N_{jf} \\ N_{af} \\ N_{jm} \\ N_{am} \end{bmatrix}_t = \begin{bmatrix} 0 & f_f & 0 & 0 \\ S_{jf} & S_{af} & 0 & 0 \\ 0 & f_m & 0 & 0 \\ 0 & 0 & S_{jm} & S_{am} \end{bmatrix}_{t-1} \begin{bmatrix} N_{jf} \\ N_{af} \\ N_{jm} \\ N_{am} \end{bmatrix}_{t-1} + \begin{bmatrix} 0 \\ I_{af} \\ 0 \\ I_{am} \end{bmatrix}_t$$

where  $N_t$  represented the number of individuals in each age-sex class,  $S_t$  was the age-sex specific survival rate, and  $f$  was the sex-specific fertility, and  $I$  was the sex-specific number of adult immigrants added to the breeding population at time  $t$ . Immigration,  $I_t$ , was treated as a random effect, or time-varying parameter. At each time step, the number of immigrants was modelled using a zero-inflated uniform distribution parameterized as:

$$I_t = \begin{cases} 0, & \text{with probability } \sim 0.5 \\ \text{Uniform}(1, 3000) & \text{with probability } \sim 0.5 \end{cases}$$

The number of immigrants estimated at time step  $t$  was added to the population size at time step  $t$ , and became part of the state-space at that time because they were available to be counted, but did not contribute to the population previously. In addition, we assumed that immigrants only moved into the population as breeding adults, and the estimated number of immigrants was added to the adult male and female class assuming equal sex ratios. Immigration was only included in the two open population models, and was excluded from the two closed population models, described in detail below.

Each state process model was linked to the count data from the ACP surveys through an observation process model. The aerial survey was conducted on the breeding grounds, prior to nesting; therefore, the survey only detected adult birds (age 2+) (Frederickson 2001, Quakenbush et al. 1995). The observation process model for each state process model was:

$$\begin{bmatrix} c_{jf} \\ c_{af} \\ c_{jm} \\ c_{am} \end{bmatrix}_t = [p_{jf} \quad p_{af} \quad p_{jm} \quad p_{am}]_t \begin{bmatrix} N_{jf} \\ N_{af} \\ N_{jm} \\ N_{am} \end{bmatrix}_t$$

where  $c_t$  represented the number of animals counted in each age-sex class, and  $p_t$  was the detection probability of individuals. Because the aerial survey only detected adult birds, the probability of detecting juveniles,  $p_{jf,jm} = 0$  and therefore,  $c_{jf,jm} = 0$ . Otherwise, detection probability,  $p_t$ , was modelled using a beta distribution with  $\mu = 0.3$  and  $\sigma = 0.02$  to reflect additional uncertainty in detection probability (Table 1). We assumed detection probability was approximately 30% for adult Steller's eiders on the ACP aerial surveys, and that detection was relatively constant across years (Stehn and Platte 2009).

The population models were based on a two-sex, two-age structured matrix population model. Juveniles were 1-year old and annual juvenile survival rate,  $(S_{jf,jm})$  was the probability of the animal surviving from 1-year old to 2-years old. Juvenile survival of Steller's eiders was estimated to be relatively high, and we chose a prior distribution based on expert opinion, previous studies, and data on spectacled eiders to reflect the range of values that we believed to be likely (Flint et al. 2000(a), Runge 2004). In addition, we assumed juvenile survival was equal between the sexes to reduce model complexity and therefore parameter redundancy (Bailey et al. 2010, Dunham and Grand *in review*). Survival of eiders prior to their first birthday (i.e., duckling & immature survival) was accounted for in the estimate of fertility ( $f_{f,m}$ ). Expert opinion and data from the Steller's eiders that nest near Barrow suggest that fertility was low, which is typical of a long-lived sea duck (Quakenbush and Suydam 1999, Quakenbush et al. 1995, Quakenbush et al. 2004, Safine 2013). Fertility was assumed to produce an equal sex ratio, and was therefore set equal between the sexes. Adult survival was the annual survival rate ( $S_{af,am}$ ) of



birds 2 years and older. Adult male survival is characteristically high, with average annual estimates from previous studies reported to range between 0.77 and 0.87 (Flint et al. 2000(b), Frost et al. 2013, Reynolds 2007). We assumed adult female survival would be lower and more variable than male survival due to the increased energetic costs and increased predation risk associated with nesting (Erikstad et al. 1998, Ghalambor and Martin 2001, Flint et al. 2000(b), Stearns 1976, Williams 1966). However, average annual survival rates of adult females from previous studies range from 0.81 to 0.90 (Flint et al. 2000(b), Frost et al. 2013, Reynolds 2007). Higher survival of females than males is uncommon in ducks species, and we believe these rates may have been higher because the studies were conducted on the molting grounds therefore including only non-breeding females. Additional uncertainty was incorporated into each of the parameter values to account for additional sampling and process variance (Figure 1, Table 1).

Four models were formulated to represent competing hypotheses about the dynamics of the Alaskan breeding population of Steller's eiders. Each model used the general state process model framework defined above. Due to the timing of the aerial surveys and the treatment of model parameters, the differences in the competing models originated in the interpretations of the observed data. The interpretations of zero count years were particularly important for Steller's eiders. For birds to be detected they must arrive at the grounds to breed; however, there were alternative hypotheses about the reason for zero count years. Models 1 and 2 assumed that the population was closed to immigration and emigration between the Alaskan breeding population and the Russian-Pacific breeding population. Models 3 and 4 assumed an open population, and therefore both models included the hierarchical time-varying parameter ( $I_t$ ), corresponding to immigration.

Model 1 assumed a closed population with no probability of a population level non-breeding event. Therefore, the only circumstance in which there could be zero birds observed was a catastrophic event causing the population to collapse. The observation model for state process Model 1 was the same as above for non-zero years, however, in zero count years  $c_t = 0$  and  $N_t = 0$ . Model 2 also assumed a closed population; however, we assumed that years in which zero birds were counted represented a population level non-breeding event. Therefore, the expected count,  $c_t$ , was allowed to equal zero in years zero birds were observed. However, unlike Model 1, a zero count year strictly represented a non-breeding event, and not a population crash. In the zero count years, the parameters ( $\theta$ ) are not updated due to the lack of data. It follows that, survival in the zero count year was equal to the survival rates estimated in the previous time step, and fertility was set to zero, to indicate non-breeding. The number of individuals in the population ( $N_t$ ), was the number of individuals expected to survive the non-breeding year.

Model 3 was reflective of a more transient population, which assumed population level emigration events corresponding with the zero count years. This was modelled using the assumption that in the zero count years, the Alaskan breeding population emigrated and joined the Russian-Pacific population. In these zero count years,  $c_t = 0$  and  $N_t = 0$ . Therefore, in years following these zero counts,  $N_t$  was entirely made up of immigrants,  $I_t$ . Years in which there were successive non-zero counts are representative of breeding birds that exhibit breeding area fidelity and constitute the Alaskan breeding population. However, in any zero count years these birds emigrated from the breeding population, resulting in  $N_t = 0$ . The estimated number of immigrant birds was added to  $N_t$  during the pre-breeding census period and were therefore accounted for in the estimated count, in any non-zero count year. If  $c_t = 0$ , both  $N_t$  and  $I_t$  were

zero because there were zero birds present. Immigration was treated as a random effect, thus it was not defined through a Markov process, and was therefore not dependent on the estimate of immigrants at any previous time step.

Model 4 also assumed an open population; however, zero count years represented a population level non-breeding event ( $f = 0$ ). Therefore, when the observation was zero,  $c_t = 0$ , but the population size  $N_t$  remains intact, and in these years there were no immigrants added ( $I_t = 0$ ). All other years allow for immigrants that were added into the resident population at the current time step. These immigrants were incorporated into the population at this time and then remain in the population throughout the time series becoming resident birds, under the assumption they were exhibiting breeding area fidelity.

Each model was fit to the available historic observation data from the aerial surveys on the ACP using Sequential Importance Sampling with Resampling that simultaneously estimated population size  $N_t$ , and both time invariant ( $\theta$ ) and time varying ( $I_t$ ) model parameters.

### *Fitting the population models*

We estimated the demographic parameters, population size, and dynamics that most likely described the observation data from the ACP surveys. There are several inferential procedures that can be used to estimate both parameters and population size including, but not limited to Sequential Monte Carlo (Doucet et al. 2001) and Markov Chain Monte Carlo (MCMC; Gilks et al. 1996) methods. Newman et al. (2009) compared both Sequential Importance Sampling (SIS) and MCMC methods for making inference about unknown states and parameters of Bayesian state-space models for British grey seal (*Halichoerus grypus*) meta-population and simulated data for a Chinook salmon (*Oncorhynchus tshawytscha*) population. Although MCMC

methods are more commonly implemented in deriving inference from SSM's, Newman et al. (2009) suggests that both methods are useful for analyzing time-series observation data. While MCMC typically produced results with less MC variation, they were also more difficult to implement and, in the case of complex models, may require employing a simpler model. Sequential Importance Sampling algorithms are typically very easy to implement, are computationally and statistically efficient, and offer the posterior distributions after each intermediate time step, providing a useful diagnostic for model deficiencies.

The SISR algorithm is initialized by generating a large number  $X$  of “particles” or samples from the prior distribution on the parameters,  $g_0(\theta_0^x)$ , and the initial state distribution  $g_0(N_0^x|\theta_0^x)$ , which generates  $g_0(N_0^x, \theta_0^x)$ . We chose  $X = 500,000$  particles, where  $x = 1, \dots, X$ . Each particle,  $x$ , represents a single realization of the demographic parameters,  $\theta_t^x$  combined with a single realization of the population  $N_t^x$ . Each particle is projected forward to  $t = 1$ , generating the state pdf  $g_1(N_1^x|N_{0:t-1}^x, \theta_1^x)$ . The particles are assigned weights proportional to the likelihood of the observation at  $t = 1$ ,

$$w_1^x w_1^x w_1^x \propto \frac{f_1(c_1|N_1^x, \theta_1^x) * g_1(N_1^x|N_{0:t-1}^x, \theta_1^x)}{g_1(N_1^x|N_{0:t-1}^x, \theta_1^x)}.$$

Each particle is resampled according to its associated weight  $w_t^x$ , using a bootstrap filtering technique (Gordon et al. 1993). The parameter distributions are then kernel-smoothed using a multivariate normal distribution, to mitigate the issue of particle depletion (Dunham and Grand *in review*, Newman and Lindley 2006, Newman et al. 2009, West 1993a,b). The parameters are transformed to the real number line,  $R^1$ , before smoothing and back-transformed afterwards. The survival rates were logit-transformed, and the fertility rates were square-root transformed to ensure normality. For each particle,  $N_t^x$  is redefined as the weighted resampled state, and the parameters  $\theta_t^x$  are redefined as the resampled and smoothed values. The resulting particles are

used to generate the prior distribution at the subsequent time step, following a first-order Markov process. This procedure is repeated sequentially through the final time step of available observation data, using the state process distribution to project forward to the next time step, then adjusting the resulting predicted state distribution using the weighted resample according to the observation process, followed by kernel smoothing the parameter distributions. For additional information on the methodology, refer to Doucet et al. (2001), Dunham and Grand *in review*, Newman et al. (2006), and/or Newman et al. (2009) for more detailed descriptions on the sequential importance sampling/resampling algorithm.

### *Model Selection*

To evaluate which model best fit the aerial survey data, we used Bayesian model weight updating. One of the primary benefits of SISR is the production of posterior estimates at each time step (Newman et al. 2009). This provides an estimate from each model, for each year, which can then be used to evaluate the fit of the models to each year of available data. Initially, each model was assigned equal weight. Using Bayes' theorem, the model weights were updated sequentially, given the prediction provided by each model compared to the actual observation from that year:

$$P(model_t^j | data_t) = \frac{P(model_{t-1}^j) * P(data_t | model_t^j)}{\sum_j P(model_{t-1}^j) * P(data_t | model_t^j)}$$

where  $P(model_t^j | data_t)$  is the model weight for model  $j$  in time step  $t$ ,  $P(model_{t-1}^j)$  is the prior probability of model  $j$ ,  $P(data_t | model_t^j)$  is the likelihood of the data given the model, and  $data_t$  is the actual observation from the aerial survey at that time step. This method was used in similar applications by McGowan (2015) and Robinson et al. (*in press*) to compare multiple

competing models of population dynamics using sequential observation data. Additionally, this approach was discussed in Barker and Link (2013) and in Hooten and Hobbs (2015). The models, SISR algorithm, and analysis were coded using MATLAB version 8.4.0.15 (The Mathworks, Inc., Natick, Massachusetts, United States).

## **Results**

The expected annual counts from each model indicate that Models 1 and 2, which represented closed systems, did not fit the observations well, likely due to the inability of the closed model predictions to vary enough to capture the variability of the data (Figure 1). Models 3 and 4, which characterized open populations, tracked well with the aerial survey data (Figure 1). While the annual estimates for Models 3 and 4 both seemed to fit the data, the results of the model weight updating suggested that Model 4 fit the data the best (Figure 2). The combined results of the SISR algorithm and the Bayesian model weight updating strongly support that the Alaskan breeding population is an open population, with movement between the Alaskan and Russian-Pacific breeding populations.

Considering the overwhelming support for Model 4 as the most likely population process model, we focused on the results from Model 4. The posterior results at the final time step for the parameter estimates from Model 4 indicated that adult survival and fertilities may be lower than previously expected (Figure 33, Table 1). The posterior on juvenile survival rates remained very similar to the prior distribution. Despite the large distribution over which the algorithm had to choose from for each demographic parameter, the posteriors for the time-invariant parameters were similar although more precise than the priors.

Because the time-varying parameter  $I_t$  was treated as a random effect, and therefore did not evolve over time, we report the weighted, resampled posterior for three time periods (Figure 4). These three time periods were chosen because they represent the variability in the estimated number of immigrants. The prior distribution on  $I_t$  was roughly half non-zero particles, over a uniform distribution from 1 to 3000 individuals (Figure 4). In 1997, which immediately followed a non-breeding (i.e., zero count) year, and a generally stable population, the estimated number of immigrants was very low ( $<300$ ), with a high probability (approximately 85%) of there being zero immigrants (Figure 1). In 1995, the posterior estimate of immigrants suggests there was about a 50% probability of zero immigrants, but the remainder of the distribution suggested that there were likely between 300 and 600 immigrants. In 2004, the posterior distribution was heavily skewed toward an immigration event. The probability of zero immigrants was very small (approximately 15%), suggesting that the observation from this year (following successive low count years) was very likely the result of a relatively large number of immigrants, approximately 600 to 1100 individuals.

## **Discussion**

To properly and efficiently monitor and manage a species, it is critical to understand the population's dynamics, and most importantly, understand the fundamental structure and underlying processes that govern the population. Bayesian state-space models provide a flexible framework to incorporate multiple sources of uncertainty while addressing competing models of population process. For further analysis of population status and trend required for Steller's eiders, an appropriate model of population process is necessary. Previous attempts at estimating population trend and extinction risk suggest that to effectively model population dynamics, one

must allow for movement between the larger Russian-Pacific population and the Alaskan population, otherwise predictions from these models will be inaccurate (J. Runge *pers. comm.*).

Our results indicate that the most likely process model includes both immigration and non-breeding events, and therefore, it will be necessary to include these events in projection models for predicting future population states and estimating extinction risk. In addition, previous studies of the three geographically distinct breeding populations suggest that there is no significant genetic differentiation between the Alaskan and Russian-Pacific breeding populations (Pearce et al. 2005). While there may not have been sufficient time since de-glaciation for significant genetic differences to evolve, these results are consistent with movement between the two breeding populations, providing additional support for our conclusion that the Alaskan breeding population is open.

This conclusion is evident based on model weight updating after the first two years of observation data. At this point, Models 3 and 4 provided the best fit to the data (Figures 1 and 2). Following the first set of zero count years in 1996 and 2000, Models 3 and 4 were the only models that were able to fit the observations because they included immigration (Figure 1). This was expected because a species with such low fertility would be highly unlikely to recover from zero years or successive low count years from recruitment alone. The high variability in the number of observed birds, combined with the extremely low fertility rates of this species, points to frequent supplementation to the Alaskan population through immigration from the Russian-Pacific population.

Model 4 gained the majority of the weight following updates based on data from 1997 because the high count in 1999 was better explained by a resident population and a large influx of immigrants. Model 3 was representative of a population that was predominantly transient; the



algorithm was unable to provide an adequate estimate of the 1999 count based entirely on immigrants. Biologically, an entirely transient population is relatively unlikely, specifically in waterfowl which typically exhibit high breeding area fidelity (Anderson et al. 1992). The support for Model 4 over Model 3 provides further evidence for breeding area fidelity by the Alaskan breeding population. While there is some evidence for this behavior (D. Safine, *pers. comm.*), and it is typical in sea duck species (Mallory 2015, Phillips and Powell 2006), the low and highly variable breeding numbers and difficulty associated with tracking these birds over multiple years, has made it extremely challenging to estimate breeding area fidelity for this population.

Periodic non-breeding has been observed in Steller's eiders near Barrow (Quakenbush et al. 2004) and in Russia on the Lena River (Solovieva 1999), and in common eiders (*S. mollissima*) in Northumberland (Coulson 1984, 2010), making it an important parameter to incorporate into population models. However, in some years when zero birds were counted on the ACP survey, some birds were present and bred near Barrow (Safine 2013). Their number and distribution appears to have been very limited, and would not be sufficient to explain the large number of breeding birds present in subsequent year. Thus, our conclusions would be unaffected. Speculation regarding the factors influencing these non-breeding events in Steller's eiders include associations with high lemming density, nesting pomarine jaegers (*Stercorarius pomarinus*), and snowy owls (*Bubo scandiacus*) (Quakenbush et al. 2004). Correlation of non-breeding with low lemming density is based on hypotheses that, in years with high lemming density, the lemmings provide an alternative prey source for predators of eiders (Quakenbush et al. 2004). Non-breeding in correlation with high density of nesting pomarine jaegers and snowy owls have been suggested because these species are highly territorial of their nests and may provide protection for neighboring Steller's eiders (Quakenbush et al. 2004). Additional

explanations for non-breeding events in eiders may be related to food availability, climate change impacts, and/or oceanic regime shifts, where non-breeding may be a strategy to reduce the risk of mortality associated with breeding when in poor condition (Coulson 1984, 2010). Cross-seasonal effects of nutrient availability and storage have been shown to affect breeding success in common eiders (Lehikoinen et al. 2006, Descamps et al. 2010) and oceanic regime shifts have been shown to be correlated with population changes in eider species (Coulson 2010, Flint 2013). It is possible that oceanic conditions and relative seasonal climate may have strong effects on the overall body condition and therefore breeding probability of Steller's eiders, because they are inextricably linked to the ocean for the majority of their food resources (Frederickson 2001, Flint 2013). The cross-seasonal and carryover effects of climate, regime shifts, and resource availability on breeding are extremely complex and vary among species and location (Alisaukas and Devink 2015, Flint 2013). These effects could be important ecological mechanisms behind the non-breeding events of this population, and additional studies regarding their effects on breeding of this population would be invaluable to the greater understanding of this population's dynamics. Although it remains difficult to say with any certainty what ultimately causes periodic non-breeding, the results of this modelling effort are supportive of periodic population level non-breeding.

This species is characteristically long-lived, with high adult survival, and low fertility (Frederickson 2001). Previous studies and expert opinion informed the prior distributions on the demographic rates, therefore providing reasonable estimates and relative uncertainty in these rates (Flint et al. 2000(b), Frost et al. 2013, Reynolds 2007). However, survival estimates for adults were based on studies that included largely non-breeding adults at Izembek Lagoon, Alaska (Flint et al. 2000(b), Frost et al. 2013, Reynolds 2007). We would expect lower survival

for breeding adults because of the relative costs associated with reproduction (Williams 1966). Posterior estimates of mean adult survival of both sexes were significantly lower than values estimated from previous studies (Table 1) (Flint et al. 2000(b), Frost et al. 2013, Reynolds 2007). These low survival rates may indicate that the studies conducted on the molting grounds are not truly representative of the Alaskan breeding population, and that this population has considerably lower survival than the larger Russian-Pacific population. The mean posterior estimate for fertility was also lower than expected (Table 1). While low fertility is common amongst long-lived sea ducks, these results are surprising because predator control, primarily fox control, was implemented in 2005 to increase fertility and adult female survival (Savory et al. 2009, 2010). This may indicate that fox control either did not affect the demographic rates, or the effect was not significant enough to detect through the observed data. There could also be an unidentified relationship with removal of foxes and an increase in nest predation from avian predators which would offset any positive effect on nest survival. Additional explanations for lower demographic rates could be attributed to a population breeding on the periphery of its range. Öst et al. (2016) found that common eiders breeding along the eastern edge of their range had significantly lower reproductive success than a population breeding in the core of their range. Low fertility may be the result of negative impacts on survival immature birds once they leave the breeding grounds (birds younger than 1 year old). Local climate issues on breeding and wintering sites may not only affect non-breeding behavior, but also negatively impact survival of young birds which would lead to reduced fertility rates (Mallory 2015). It is difficult to point to one specific cause of such low fertility, and it may be that it is caused by any combination of factors that exacerbate the overall effects of predation and climate on fertility.

Current recovery criteria for the Alaskan breeding population rely heavily on the ability to estimate population viability in the future (USFWS 2002). This modelling effort provides an informative model of population process that can be used to examine future population trends and assess the population in terms of the current recovery and reclassification criteria. Previous attempts to quantify population viability and trend concluded that the Alaskan breeding population was declining (Stehn et al. 2013, J. Runge *pers. comm.*). However, J. Runge (*pers. comm.*) suggested that, without accounting for dispersal from the larger Russian-Pacific population, these results were likely an inaccurate representation of the population. The results of this modelling effort demonstrate that immigration and periodic non-breeding are necessary to explain the observations, and therefore should be included in any predictive modelling of this population to obtain accurate estimates of population viability.

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## Tables and Figures

**Table 2.1.** Prior mean, standard deviation, and distribution for the parameters used to initialize each model. Posterior mean and standard deviation are reported the final time step (year 2013) from Model 4.

Parameter	Prior	Prior	Prior Distribution	Posterior	Posterior
$\theta$	$\mu$	$\sigma$	$g_0(\theta)$	$\mu$	$\sigma$
$f_{f,m}^a$	0.009	0.03	<i>beta</i> (0.085, 18.82)	0.0062	0.00015
$S_{jf,jm}^b$	0.75	0.10	<i>beta</i> (13.31, 4.43)	0.748	0.011
$S_{af}^c$	0.80	0.10	<i>beta</i> (12, 3)	0.754	0.015
$S_{am}^c$	0.85	0.075	<i>beta</i> (18.42, 3.25)	0.81	0.009
$p_t^d$	0.30	0.02	<i>beta</i> (157.2, 366.8)	--	--

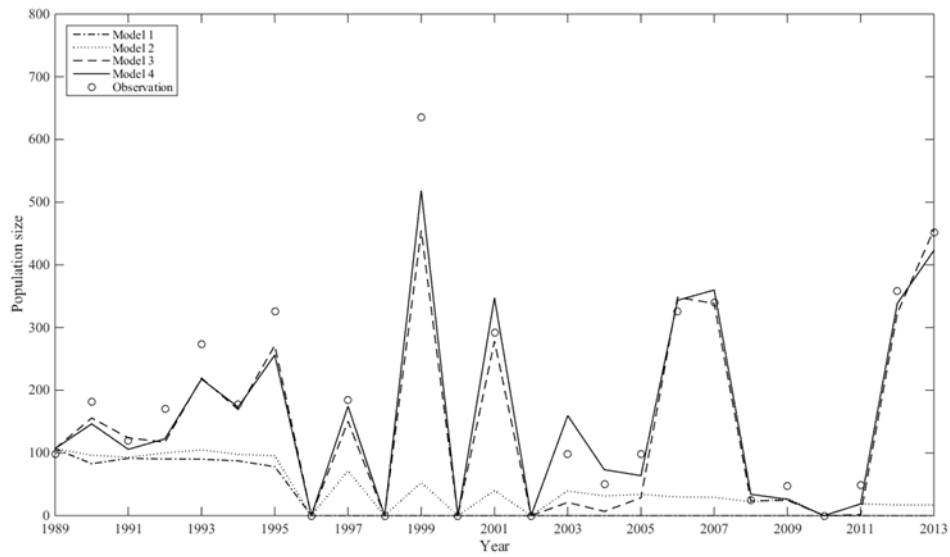
*Note:*  $S$  indicates sex and age specific survival,  $f$  indicates sex specific fertility, and  $p$  indicates detection rate.

<sup>a</sup> Mean fertility from estimates in Safine (2013), Quakenbush and Suydam (1999), Quakenbush et al. (1995), Quakenbush et al. (2004), and J. Runge *pers. comm.* Additional error was incorporated into the prior standard deviation to account for process and sampling error.

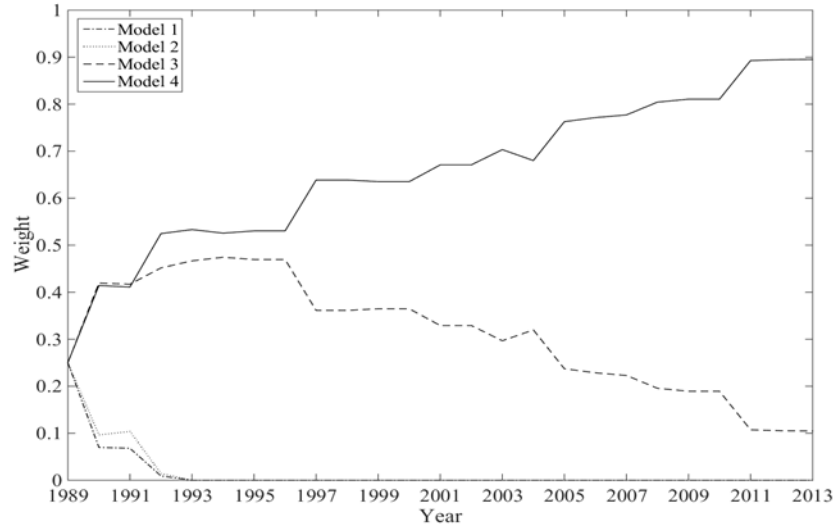
<sup>b</sup> Estimated juvenile survival based on expert opinion.

<sup>c</sup> Adult survival taken from Flint et al. (2000), Frost et al. (2013), and Reynolds (2007). Additional error was incorporated into the prior standard deviation to account for process and sampling error.

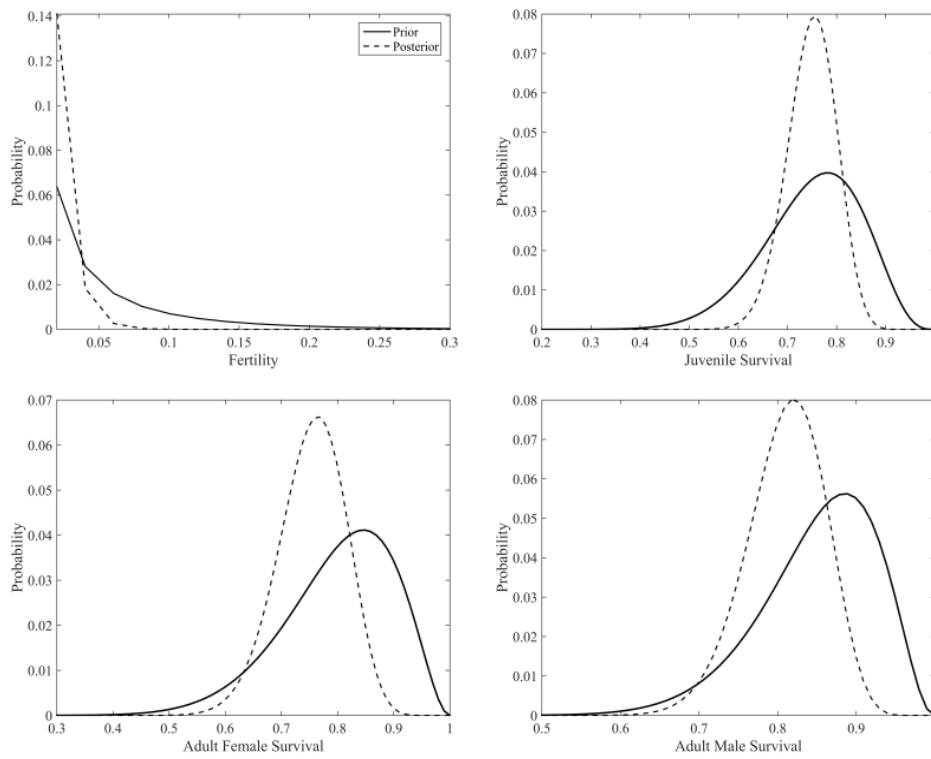
<sup>d</sup> Detection rate assumed to be relatively constant (Stehn and Platte 2009), incorporated additional error to account for process and sampling error.



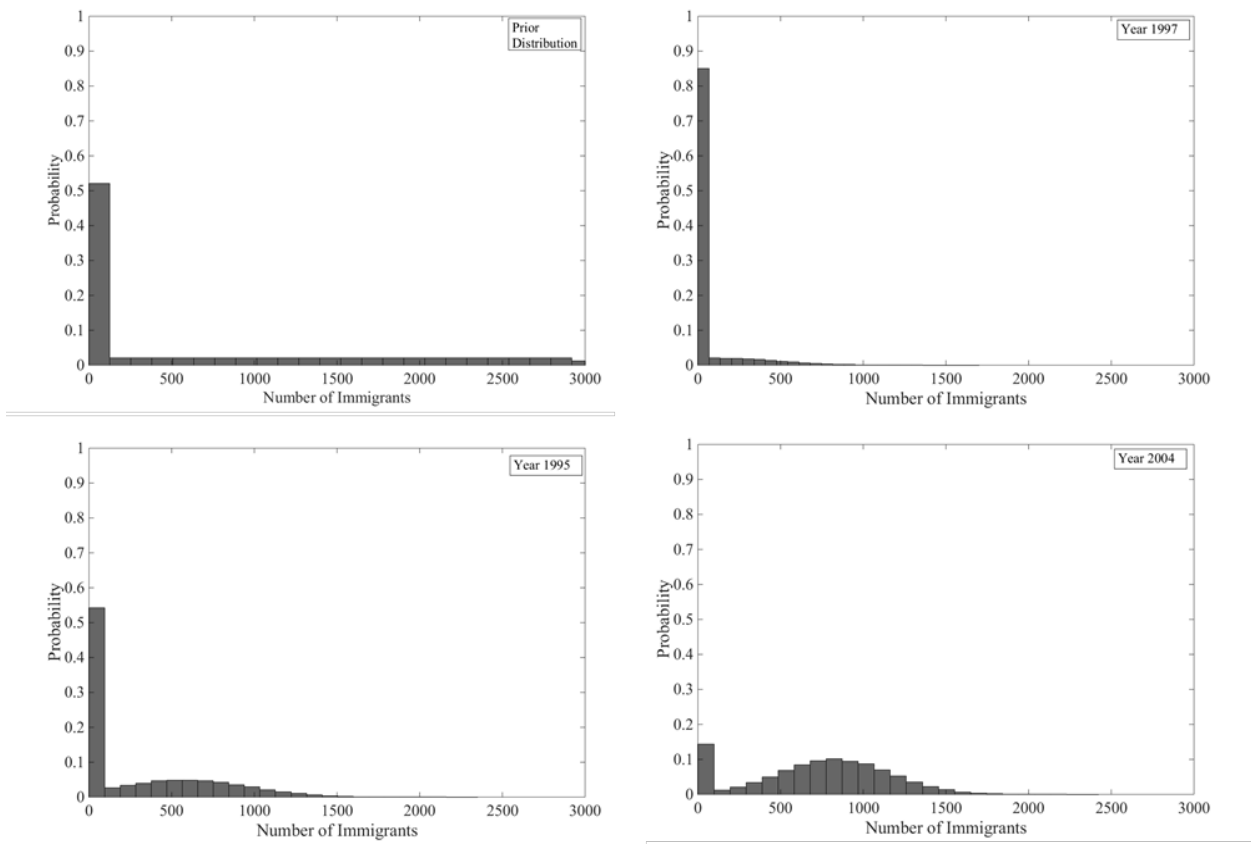
**Figure 2.1.** Posterior means of expected counts from SISR for four candidate models compared to annual estimated counts from aerial surveys of Steller's eiders on the Arctic Coastal Plain of Alaska from 1989 to 2013. Models 3 and 4 fit the observed data closely, and represented open population models, while Models 1 and 2 were closed population models and were unable to track with the highly variable observations.



**Figure 2.2.** Model weight evolution from Bayesian updating for four candidate models of Steller’s eider populations on the Arctic Coastal Plain of Alaska from 1989 to 2013. Although both Model 3 and 4 produced reasonable count estimates, Model 4 outperformed all of the other models.



**Figure 2.3.** Prior and posterior distributions for fertility and survival rates. Posterior distributions are from the final time step (year 2013) from Model 4. Posterior means were lower and more precise than priors for each parameter.



**Figure 2.4.** Prior and three posterior distributions for immigration ( $I_t$ ) from Model 4. The prior distribution is a zero inflated uniform distribution, and the posterior distributions are representative of years with low (1997), medium (1995), and high (2004) probability of immigrants.

## Chapter 3:

### Population viability of the Alaskan breeding population of Steller's eiders

#### Abstract

The U.S. Fish and Wildlife Service is tasked with setting objective and measurable criteria for delisting species or populations listed under the Endangered Species Act. Determining the acceptable threshold for extinction risk for any species or population is a challenging task, particularly when facing marked uncertainty. The Alaskan breeding population of Steller's eiders (*Polysticta stelleri*) was listed as threatened under the Endangered Species Act in 1997 due to a perceived decline in abundance and nesting range and geographic isolation from the Russian breeding population. However, previous genetic studies and modeling efforts suggest that there may be dispersal from the Russian breeding population. Additionally, there is evidence of population level non-breeding events. This research is aimed to estimate population viability of the Alaskan breeding population of Steller's eiders using both an open and closed model of population process for this threatened population. Projections suggest under a closed model of population process this population has a 100% probability of extinction within 42 years. Projections from the open population model suggest that with immigration there is no probability of permanent extinction. However, due to random immigration process and non-breeding behavior it is likely that this population will continue to be present in low and highly variable numbers on the breeding grounds in Alaska. Monitoring the winter population, which contains

both Russian and Alaskan breeding birds, may offer a more comprehensive indication of population viability.

## **Introduction**

The U.S. Fish and Wildlife Service is tasked with setting objective and measurable criteria for delisting species or populations listed under the Endangered Species Act. These criteria are described within a Recovery Plan, which serves as a guide for the management and recovery of threatened and endangered species. Common recovery criteria include assessing the imperiled population in terms of extinction risk, and setting extinction risk thresholds that once reached indicate when the population can be delisted. Determining the acceptable threshold for extinction risk for any species or population is a challenging task, particularly when facing marked uncertainty. This becomes increasingly difficult when considering that imperiled species are typically rare or uncommon at the time of listing, and generally little is known about their biological or population processes. Assessing a population's risk of extinction requires in depth knowledge of the populations processes and dynamics. If applicable, these processes may include interactions with nearby populations of the same species. Considering the potential influence of exchanges between two or more populations may be imperative to determining persistence or extinction risk.

Species or populations listed under the Endangered Species Act typically face an increased risk of extinction due to any host of factors. The Alaskan breeding population of Steller's eiders (*Polysticta stelleri*) was listed as threatened under the Endangered Species Act in 1997 due to a perceived decline in abundance and nesting range and geographic isolation from the Russian breeding population (Federal Register 1997, Pearce et al. 2005). The Alaskan



breeding population is the smallest of three geographically distinct breeding populations of Steller's eiders (Frederickson 2001, U.S. Fish and Wildlife Service 2002, Pearce et al. 2005).

A Recovery plan was drafted for the Alaskan breeding population of Steller's eiders in 2002, defining the listed "population" as any Steller's eiders that breed in Alaska, and the term "subpopulation" to mean a group of Steller's eiders that form a geographic subunit of the Alaska breeding population (USFWS 2002). According to the recovery plan, there are two subpopulations of Steller's eiders, denoted as the northern and western Alaskan subpopulations (USFWS 2002). One of the primary reasons for listing the Alaskan breeding population was the near extirpation of the western subpopulation along the Yukon-Kuskokwim Delta (USFWS 2002). Since the mid-1970's, only 7 nests have been found on the Yukon-Kuskokwim Delta , with no indication of an established population (Kertell 1991, Flint and Herzog 1999, USFWS 2002). The recovery criterion for delisting and reclassification from threatened to endangered includes considerations of the viability of both subpopulations (USFWS 2002). However, due to the lack of any evidence of breeding birds in the western subpopulation, we cannot consider the western subpopulations influence on overall population viability. Therefore, we will focus on assessing the viability of the northern subpopulation of Alaskan breeding Steller's eiders within the current recovery criteria from the recovery plan (USFWS 2002).

Population viability analysis (PVA) is a tool commonly used to evaluate population persistence and estimate extinction risk (Shaffer 1990, Boyce 1992, Goodman 2002, Morris and Doak 2002, Robinson et al. 2014). Additionally, metapopulation viability analyses assess viability in systems that are composed of interacting local populations that are open to immigration and emigration events. This approach accounts for migration amongst these local populations and its effect on dynamics, most importantly, this allows for the possibility of

recolonization following a local extinction (Levins 1974, Hanski and Simberloff 1997). These populations can exhibit source-sink dynamics, in which there are populations that births outnumber deaths (source populations) and populations where deaths outnumber births (sink populations) (Hanski and Simberloff 1997). These dynamics have critical implications for the assessment of local population viability, and therefore conservation and management of any local population within a metapopulation. Population and metapopulation viability analyses are used to estimate the future state of the population(s), and quantify the probability of persistence or extinction (Goodman 2002, Morris and Doak 2002).

The Alaskan breeding population of Steller's eider nests primarily on the Arctic Coastal Plain, annual aerial surveys from 1989 to 2013 indicated that Steller's eiders were present in low and highly variable numbers, with multiple years resulting in estimated counts of zero (Kertell 1991, Pearce et al. 2005, Stehn and Platte 2009, Stehn et al. 2013). Using the aerial survey data set in previous work, we sought to develop and evaluate competing models of population process to determine the most likely process model for the Alaskan breeding population (Dunham and Grand *in prep*). Results indicated that the Alaskan breeding population is likely open to immigration from the nearby Russian-Pacific breeding population and experiences population level non-breeding events (Dunham and Grand *in prep*). The dispersal of individuals from the Russian-Pacific breeding population to the Alaskan breeding population will likely have profound consequences for assessing the viability of the listed population. Additionally, the years in which zero birds are present on the breeding grounds presents further challenges regarding extinction risk. The years in which there are zero birds documented would typically qualify as years in which the population was extinct, followed by recolonizations of the breeding area. However, this behavior is believed to be representative of periodic non-breeding, a strategy

employed by many long lived species, including eiders (Coulson 1984, Quakenbush et al. 1995, Solovieva 1999, Obritschkewitsch et al. 2001, Quakenbush et al. 2004, Coulson 2010, Safine 2013).

While our previous work strongly supports that this population is open to immigration and non-breeding events, there are still alternative hypotheses that suggest this is a closed population. Therefore, this research is aimed to estimate population viability of the Alaskan breeding population of Steller's eiders using both an open and closed model of population process for this threatened population.

## **Methods**

### *Population Models and Parameterization*

In previous work, we developed and evaluated multiple models of population process and estimated key demographic parameters of the Alaskan breeding population (Dunham and Grand in prep). We fit these models to annual aerial survey data collected from the Arctic Coastal Plain (ACP) of Alaska to determine which process model(s) best fit the data, and estimated the key demographic parameters associated with each model. The best fit process model included population level non-breeding and time-varying immigration, in addition to survival and fertility of the two sexes and the juvenile and adult age classes (Dunham and Grand in prep). It has long been assumed that this breeding population is closed; however, the likelihood of population closure has never been formally evaluated. To address previous notions that this population is closed to immigration from the larger Russian-Pacific breeding population, we also assessed population viability under assumptions of population closure. While our previous work points to this breeding population being open to immigration, we chose to evaluate population viability

under both process models for transparency. Model parameters and details are described in detail below.

### Closed Population Model

We developed a two-stage, two-sex matrix population model corresponding to a pre-breeding census for the Alaskan breeding population of Steller’s eiders. We used the resulting posterior distributions for each vital rate from our previous Bayesian analysis to construct and parameterize each projection matrix model (Dunham and Grand in prep). Using the posterior probability distributions from our previous analysis allowed us to incorporate the most accurate information available while accounting for multiple sources of uncertainty. The population dynamics model for the closed population was defined as:

$$\begin{bmatrix} N_{jf} \\ N_{af} \\ N_{jm} \\ N_{am} \end{bmatrix}_t = \begin{bmatrix} 0 & f_f & 0 & 0 \\ S_{jf} & S_{af} & 0 & 0 \\ 0 & f_m & 0 & 0 \\ 0 & 0 & S_{jm} & S_{am} \end{bmatrix}_{t-1} \begin{bmatrix} N_{jf} \\ N_{af} \\ N_{jm} \\ N_{am} \end{bmatrix}_{t-1}$$

where  $N$  represents the number of individuals in each age-sex class,  $S$  is age-sex specific survival, and  $f$  is sex specific fertility. The first stage represents birds that were 1 year old and reproductively immature, and survival ( $S_{jf,jm}$ ) was set equal between the sexes. Juvenile survival was chosen from a beta distribution with mean of 0.748 and a standard deviation of 0.011 (Dunham and Grand in prep). Adult survival was the annual survival rate ( $S_{af,am}$ ) of birds 2 years and older and we assumed all adult birds (age 2+) of the same sex experienced a similar survival rate. Adult male survival was estimated to be high, chosen from a beta distribution with a mean of 0.81 and a standard deviation of 0.009 estimated from our previous analysis (Dunham and Grand in prep). Adult female survival is characteristically lower than male survival and more variable due to the increased energetic costs and increased predation risk associated with nesting

(Erikstad et al. 1998, Ghalambor and Martin 2001, Flint et al. 2000, Stearns 1976, Williams 1966). Adult female survival was pulled from a beta distribution with a mean of 0.754 and standard deviation of 0.015 (Dunham and Grand in prep). Fertility rates for the Alaskan breeding population are exceptionally low (Dunham and Grand in prep). While low fertility rates are typical of a long lived sea duck, results from our previous analysis indicate that they are lower than previously expected (Dunham and Grand in prep). Fertility rates were set equal between the sexes, and pulled from a stretched beta distribution with a mean of 0.0062 and standard deviation of 0.00015 (Dunham and Grand in prep).

### Open Population Model

The open population model used the same general framework as the closed population model, with two additional parameters. The open population model included an additional vector  $I_t$ , to represent immigration, and fertility was set dependent on a binomial random variable, breeding probability. The open population dynamics model was as follows:

$$\begin{bmatrix} N_{jf} \\ N_{af} \\ N_{jm} \\ N_{am} \end{bmatrix}_t = \begin{bmatrix} 0 & f_f & 0 & 0 \\ S_{jf} & S_{af} & 0 & 0 \\ 0 & f_m & 0 & 0 \\ 0 & 0 & S_{jm} & S_{am} \end{bmatrix}_{t-1} \begin{bmatrix} N_{jf} \\ N_{af} \\ N_{jm} \\ N_{am} \end{bmatrix}_{t-1} + \begin{bmatrix} 0 \\ I_{af} \\ 0 \\ I_{am} \end{bmatrix}_t$$

where  $I_t$  includes the number of adult female ( $af$ ) and adult male ( $am$ ) immigrants estimated at the current time step,  $t$ . This population is strictly made up of breeding birds, and more specifically breeding pairs, and therefore the number immigrants simulated in any time step is divided equally between the sexes. Additionally, because this is representative of the breeding population, and juveniles do not breed, we did not allow for juvenile immigrants in this model. Immigration,  $I_t$ , was treated as a random effect, or time-varying parameter. At each time step,

the number of immigrants was simulated from a zero-inflated Uniform distribution which we parameterized as:

$$I_t = \begin{cases} Pr(0) \sim (0.2) \\ Uniform(1, 1500) \text{ with } Pr(1 - Pr(0)) \end{cases}$$

Our previous study resulted in posterior distributions for immigration at each time step (Dunham and Grand in prep). Considering the posterior distributions from this work, we chose to use a Uniform distribution to capture the uncertainty we have surrounding the drivers of immigration. An additional constraint on immigration was set by the relationship with the non-breeding years. In our previous modelling effort, years in which zero birds were detected were representative of years that the population did not breed and did not experience any immigration (Dunham and Grand in prep). The annual surveys and our model indicated that there were 5 non-breeding years out of the 25 years of annual survey data (Dunham and Grand in prep). Therefore, the probability of a non-breeding year was roughly 20%. Furthermore, the 25 years of aerial survey data did not include any consecutive non-breeding events, and therefore we constrained non-breeding years to never occur consecutively in this model. Fertility,  $f_{f,m}$ , is defined as the number of offspring recruited to the juvenile (one-year old) age class per female annually, and is dependent on the non-breeding probability, which is parameterized as a random binomially distributed variable that returns a 0 to represent non-breeding years, and 1 for breeding years. Therefore, in breeding years, fertility was drawn from a beta distribution with a mean of 0.0062 and standard error of 0.00015, and in non-breeding years, fertility was set equal to zero. Survival rates were simulated from the same distributions described in the section above.

## *Simulations*

Both models of population dynamics were projected to 100 years using 5,000 iterations. The closed population model was initialized with an initial population size ( $N_1$ ) chosen from the following distribution:

$$N_1 \sim \text{Poisson}(\lambda)$$

where  $\lambda = 1,325$ , this distribution was reflective of the posterior distribution of population size from our previous analysis (Dunham and Grand in prep). The initial population size for the open population model was estimated by adding  $N_i$  and  $I_1$ . The initial age distribution was distributed according to the mean age distribution of the posterior results from our previous analysis, with additional variation to reflect our uncertainty in this estimate.

We were interested in comparing the projections to the metrics defined in the Recovery Plan (USFWS 2002). However, some metrics are not presently applicable, according to the current wording of the Recovery Plan. For this reason we are only interested in the metrics that are currently applicable to this population. Therefore, we calculate the : (1) the probability of quasi-extinction, (2) time to quasi-extinction, (3) probability of local extinction and, (4) time to local extinction for the open and closed population models, and (5)  $\lambda$  (population growth rate) for the closed population model. Quasi-extinction was defined as the population size being  $\leq 10$  individuals and the time to quasi-extinction was defined as the year in which the population size of every iteration had reached 10 individuals or less. Extinction was defined as the population size being 0 individuals and time to extinction was the year in which every iteration had reached 0 individuals.

## **Results**

The closed model resulted in a 100% probability of quasi-extinction within 29 years, and 100% probability of extinction within 42 years (Figure 1). The open population model resulted in 19.28% of the iterations reaching the quasi-extinction threshold of 10 individuals, and 0.006% of the iterations reaching extinction at some point in the 100 years of projection. Because this population occurs in low and highly variable numbers on the breeding grounds, there is still some expectation that this local population will experience temporary decreases in population size. However, because of frequent immigration, there is no probability of long-term or permanent quasi-extinction or extinction for this breeding population. Due to the rescue effect of immigration, it is not possible to measure a time to quasi-extinction or time to extinction, because there was no time in which all iterations reached either threshold (Figure 1).

## **Discussion**

Without the reintroduction or recolonization of the Yukon-Kuskowim Delta by the western subpopulation of Alaskan Steller's eiders or the designation of the subpopulations as distinct vertebrate population segments, the recovery criteria as listed in the plan cannot be met (USFWS 2002). However, we sought to assess the viability of the northern subpopulation of Alaskan breeding Steller's eiders using two models. The results of the closed population projections suggest that the population would rapidly decline and become extinct within 42 years, and would therefore qualify to be reclassified as Endangered, according to the current recovery criteria (Figure 1). While our previous models suggest a closed model is an unlikely representation of this population process, we included this model for transparency. Additionally, previous studies of the geographically distinct breeding populations (Russian-Atlantic, Russian-



Pacific, and Alaskan) suggest there is no significant genetic differentiation between the Alaskan and Russian-Pacific breeding populations (Pearce et al. 2005). The results of these studies illustrate that it is highly unlikely that this breeding population is closed because the productivity and survival rates do not support a self-sustaining population. This information is critical for the management and monitoring of this listed breeding population.

The Alaskan breeding population was listed due to perceived declines in abundance in their nesting and breeding range, specifically along the Yukon-Kuskokwim Delta (USFWS 2002). One of the primary objectives listed in the Recovery Plan was to gather more information on breeding population dynamics to assess population viability (USFWS 2002). Analysis of 25 years of aerial survey data indicate that this population has been rescued through immigration events and experiences intermittent breeding (Dunham and Grand in prep). Given this updated understanding, we believe the model put forth in this research is the best available representation of population process and dynamics. The mean projected results from this model indicate that the Alaskan breeding population will likely remain relatively stable throughout the next 100 years, with no probability of permanent local extinction; however, this is dependent on immigration (Figure 1). The outcome of this study combined with those from our previous research, suggest that immigration plays a critical role in the population dynamics and consequently the viability of the Alaskan breeding population of Steller's eiders (Dunham and Grand in prep).

Our previous study highlighted the importance of immigration in accounting for the highly variable observed counts of the breeding population on the Arctic Coastal Plain (Dunham and Grand in prep). Furthermore, this study identifies the role of immigration as being vital to the viability of the Alaskan breeding population. The significant role of immigration may be representative of source-sink dynamics. In this case, the source population would be the Russian-

Pacific breeding population and Alaskan breeding population would act as the sink. Öst et. al (2016) found that immigration played a similar role in population dynamics of Common eiders (*Somateria mollissima*) breeding in two different geographic locations in the Baltic Sea. After analyzing long-term individual-based data on eider breeding success and survival, they detected these dynamics because this population segments offspring production was not high enough to explain the population growth during the times of rapid increase (Öst et. al 2016). In addition, the location which experienced low reproductive success and speculated immigration is located in the eastern range margin and not in what is thought to be the core breeding range (Öst et. al 2016). While Common eiders do exhibit strong breeding site fidelity, Öst et. al (2016) believes natal dispersal could be a strong driver of the apparent source-sink dynamics. Similarly, our previous research indicated that the best model of population process allowed for birds to enter the population, but at that point they remained in the population to mimic breeding site fidelity (Dunham and Grand in prep). Furthermore, Steller's eiders are thought to prospect for breeding sites in the year previous to becoming sexually mature. Considering that most eider species exhibit breeding site fidelity, but results indicate immigration is an important mechanism in regulating population dynamics, it is likely that natal dispersal plays a large part in providing immigrants to the Alaskan breeding population.

Mean population projections suggest a relatively stable population, however, it is probable that the northern subpopulation of Steller's eiders will continue to be present in low and highly variable numbers on the ACP breeding grounds (Figure 2). Typically, local extinction would be defined as any time in which there were zero individuals of that population in the designated geographic area. In the case of this breeding population, the probability that the population will not breed and consequently not be detected on the aerial surveys is ~20%

(Dunham and Grand in prep). Therefore, over the course of the next 100 years the breeding population would likely be designated as extinct under this definition. Currently, there is no definition of what would constitute local extinction for this breeding population in the Recovery Plan (USFWS 2002). It may be important to reconsider what quantifiable metrics apply to this highly variable population.

While results strongly support that this breeding population is open to immigration and experiences population level non-breeding events, we do not know what factors directly influence these occurrences. Further research is needed to identify what factors drive these important biological processes. Previous studies have indicated that there may be a relationship between breeding probability and density of lemmings, pomarine jaegers (*Stercorarius pomarinus*), and snowy owls (*Bubo scandiacus*) (Quakenbush et al. 2004). However, direct links of the effects of interspecies relationships to breeding probability in Alaskan breeding Steller's eiders have not been established. Additional hypotheses for causes of intermittent breeding in eider species may be linked to environmental factors, including direct and indirect effects of climate and/or oceanic regime shifts that alter food availability (Coulson 1984, 2010). If breeding of Steller's eiders is linked to species specific densities on the breeding grounds or by environmental factors that influence survival and/or breeding probability, we may be able to better predict their effects on population viability in the future. However, it is likely that as long as there is an available pool of immigrants from the Russian-Pacific population, then the Alaskan breeding population will persist.

Our results suggest that immigration is necessary to sustain the Alaskan breeding population of Steller's eiders. We demonstrated that the variability on the breeding grounds and population viability of this breeding population are influenced by intermittent breeding and

dispersal from the Russian-Pacific breeding population (Dunham and Grand in prep). While there is little information on the Russian-Pacific breeding population, we do know that they share molting and wintering grounds in southwestern Alaska with the Alaskan breeding population (Dau et al. 2000, Flint et al. 2000, Larned 2012, Frost et al. 2013, Martin et al. 2015).

Additionally, previous studies found that both sexes showed high rates of fidelity to specific molting sites (Flint et al. 2000). This provides a unique opportunity to monitor both breeding populations on the molting and/or wintering grounds, to gain a more comprehensive understanding of metapopulation dynamics. Analysis of aerial surveys conducted from 1992 to 2010 on the spring staging areas along the Bristol Bay coast of the Alaskan Peninsula indicate that the long-term trend is an exponential decline of 2.4 percent per year (Larned 2012). This apparent decline of the number of staging birds warrants further research and monitoring as this may indicate whether the metapopulation viability is at risk, which could increase the permanent probability of extinction of the Alaskan breeding population.

Finally, one of the most challenging issues faced when managing this species has been estimating population size and/or trend because of the difficulty associated with detectability. Throughout their annual cycle they are dispersed over large geographic extents and are difficult to detect with precision. At this point we do not have recent or precise data to inform detection probability for Steller's on the aerial surveys on the ACP. Without understanding the detection process we cannot accurately estimate population size or trend. We incorporated a large amount of uncertainty in initial population size to reflect our uncertainty in this estimate. Furthermore, the annual aerial survey point count estimates are imprecise, leading to further uncertainty around population trend and size. With estimates of detection probability, we could reduce the uncertainty around each annual point count estimate, and consequently reduce the uncertainty in

population size and trend. Calculating precise estimates of detection probability on the aerial breeding ground surveys and on any surveys conducted on the molting or wintering grounds will be critical to the management and conservation of this species.

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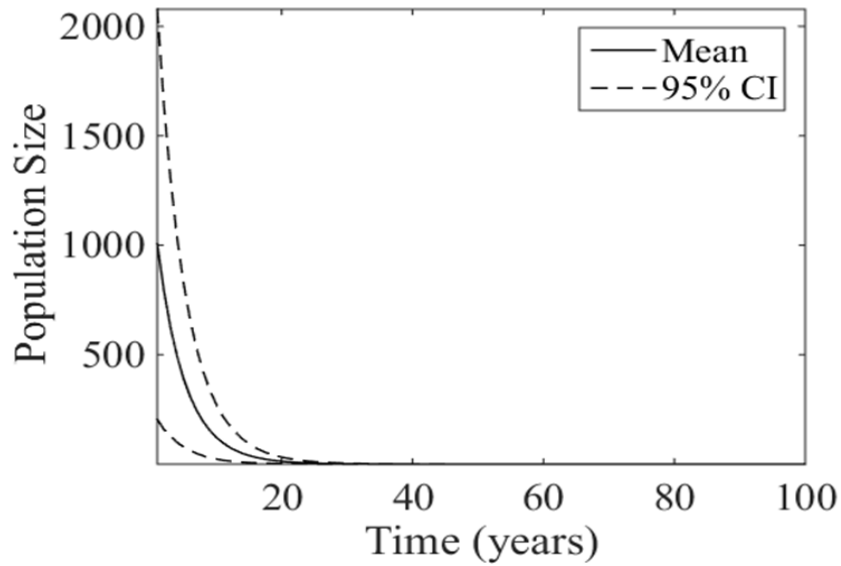
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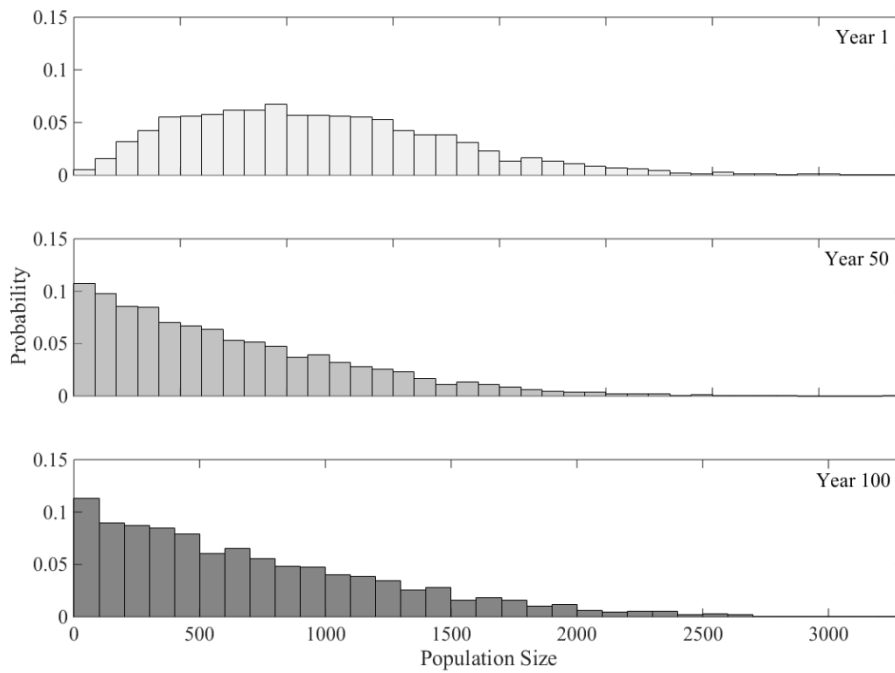


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### Tables and Figures



**Figure 3.1.** Mean population size projections with 95% credible intervals for the closed population model of Alaskan breeding Steller's eiders (*Polysticta stelleri*).



**Figure 3.2.** Prior distribution for year 1 and posterior distributions of population size from projections for years 50, and 100 from the open model of population process for Alaskan breeding Steller’s eiders (*Polysticta stelleri*). Posterior distributions are skewed heavily towards zero; suggesting very small population sizes are highly likely.